THE

LIVING SUBSTANCE

AS SUCH: AND AS ORGANISM

BY

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Supplement to JOURNAL OF MORPHOLOGY, Vol. XII, No. 2

BOSTON
GINN & COMPANY
The Athenæum Press
1897

TO

MY MOTHER,

WITHOUT WHOSE EXAMPLE OF PATIENT PERCEPTION

THESE RESEARCHES COULD NEVER HAVE BEEN MADE;—

AND

TO

MY HUSBAND,

WITHOUT WHOSE UNSELFISH ENCOURAGEMENT

THEY WOULD NEVER HAVE BEEN OFFERED TO THE WORLD;—

THIS RECORD IS DEDICATED.

"That which is is far off and exceeding deep: who can find it out?"

"Because however much a man labour to seek it out, yet shall he not find it; yea, moreover, though a wise man seek to know it, yet shall he not be able."

Ecclesiastes.

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PREFACE.

THE editing of certain studies in protoplasmic phenomena having been set aside again and again by circumstances, I am impelled to publish a somewhat condensed account of the more important facts which bear on problems of the day.

To do this is to do less justice to the work than one could wish, seeing that the larger truths presented were built up as mosaics by mere accretion of individual facts; a method forbidden by the scope of a summary when the number of facts is legion.

Yet it is possible to give a bird's-eye view of the ground covered, and, perhaps, to justify those broader statements,

which, however they may read, here and there, under such constraint as hypothesis and argument, are but summarized facts.

The work, at time of its doing, embodied an appeal to the normal, living substance, as against "preserved" and tortured states, in which the prevailing standpoint delighted, and from which even workers of physiological bias had not freed themselves.

As pioneer work it then ran sufficiently counter to prevailing enthusiasms to be in danger of harsh dealing; to-day it may hope for some scattered sympathy. A direct, independent appeal to protoplasm, *per se*, which I have been led to call in terms of my results, the living substance, as such; it was unhampered by theory or predilection, except what may be described as a belief in life-genii more complex and more potent than even surface tension and osmosis.

The work was carried on partly at the Marine Laboratory at Wood's Holl, partly at the University of Pennsylvania, and finished in the spring of 1894. It was assisted by constant study, during the preceding ten years, of many of the forms then used for specialized research. The very full memoranda made always at the moment have since been confirmed by frequent and iterated observations on the same, or closely allied, material. A few new facts gained in the course of these are omitted here, since they are in the nature of confirmation purely, and the mass of facts was already too great to be used *in toto*.

All controversial references, except a few to Bütschli's epoch-making work on protoplasm, to which I owe much, and which gave the point of departure for these researches, have been omitted, both because the work, save for this, was wholly independent, and because such reference would have increased the paper to a size unsuitable even for book form.[1]

And a controversial tone is wholly unnecessary, since the facts harmonize rather than clash with all other well-authenticated facts known to me.

[1] As an understanding of Bütschli's views is advisable for perfect comprehension of this paper, it is recommended to those who have not opportunity to read his whole work, to read a review of it by Dr. E. A. Andrews which appeared in Science, N.S., vol. II, Dec. 27, 1895. In Bütschli's magnificent work the existing theories are reviewed.

The new facts are not thought to *explain* the phenomena, but only to *unify* them, so that the future master who shall find for us an explanation may have a less incoherent mass of contradictory evidences to deal with.

Though it is felt that acknowledgment to those who have from time to time befriended the work by giving opportunities to the worker, were better left for a later and more complete presentment, which should more fully justify their faith and requite their kindness; it is impossible to omit here recognition of help without which the work might never have been done.

To Dr. Edmund B. Wilson, who in 1888 admitted me as a hearer to his class at Bryn Mawr College, I owe such technical training as I possess; and also then, and later at Wood's Holl, stimulus and inspiration to research work, such as springs naturally from contact with so gifted and catholic a mind, and such as grows under an unflagging interest and practical help given all who show interest in their work.

Through the kindness of Dr. C. O. Whitman, I occupied for three summers a room in the Investigator's Department of the Marine Biological Laboratory at Wood's Holl, Mass., and received much encouragement and stimulus, both from him personally and from the environment his scientific achievements and genial influence create, — a circle of disinterested workers who gather about him there, making an atmosphere electric with enthusiasm, and holding neither method nor result a secret from one another.[1]

Finally, the liberal practical aid of Dr. Horace Jayne, Dean of the University of Pennsylvania, providing a private laboratory in the Biological Department, greatly furthered the work and enabled me to bring it, so far as it goes, to a satisfactory conclusion during the winter of 1894. The perfect optical conditions enjoyed there, the open north light and freedom from vibrations, gained me some valuable points; and

[1] I desire distinctly to free from all responsibility for my choice of a subject, or its treatment, the above savants. The privileges and help acknowledged here were given to aid research on the embryology of rotifers, the results from which, because incomplete, are still unpublished. The present work was carried on at the same time and was known to myself only, being then but fragmentary results.

happy chance also brought within my reach in the conservatory some material specially adapted to certain of the problems.

Thanks are due also the great courtesy shown by M. Lacaze Duthiers, by whose permission I was enabled to enjoy, in the summer of 1894, the unique privileges of the Zoölogical Laboratory at Roscoff, France, and there to repeat, under most favorable circumstances, the observations on starfish and echinus eggs; upon which facts, because of their very startling nature, I should otherwise have been loath to build from one series of observations.

Methods.[1]

The optical instruments were, with one exception, of Zeiss; a Zeiss stand, largest size, and accessories; 4 mm., and 2 mm. immersion, objectives; compensating eyepieces, 4, 6, 8, 12. The exception spoken of was a picked $\frac{1}{12}$ immersion of Beck's. The work done with this was afterward verified with the Zeiss tools. The illumination was from an Abbé condenser, with at night blue glass, and a bull's-eye lens, or waxed-paper screen.

Considering the nature of the work, it should possibly be mentioned in this connection that it was further assisted by exceptionally far-sighted eyes, having great range and swiftness of accommodation.

The optical conditions were found to be of utmost importance. Pure light on a clear day, from a northern exposure, gave best results. Failing this, good artificial illumination with above conditions was preferred, with precautions against undue heat.

The work done with higher combinations was always compared, where possible, with results given by a series of lower powers; that done with lower powers was verified always under higher combinations; so that optical appearances were thus compared with their physical basis of structure. This method gave often important results.

For the more delicate structures and phenomena a sensitive adjustment of optical conditions was found to be essential, and

[1] For the reader's convenience the leading results are indicated by numbers in brackets.

slight variations in these latter, or even in the physiological state of the observer, served to hide important facts.

[1] All observations were made upon the living material, and in many instances accompanied by, and compared with, "preservation methods" of approved sorts. These latter served chiefly to show their own inadequacy, acting either as stimuli or as relaxers of the substance; so that, although one might fix beautiful structures, and even so delicate structures as those figured by Bütschli, one had not strictly the original structure, certainly not throughout the mass. The impossibility of getting reagents to fix simultaneously all parts of even small masses is a great, a serious drawback; even hot osmic fumes failing often to do more than create a compound of locally altered states of the irritable and active substance.

I have convinced myself that "preservatives" fix for us little of the true structure of the living substance, and can, at best, keep for us grosser relations, of a mixed sort in point of time; hiding an infinite complexity of form, and destroying perforce those infinitely delicate relations whose fleeting harmonies make up life phenomena. I speak of "preservation methods" of the past and present, not of the future.

They have been invaluable in awakening us to the knowledge that something we had not known lay hid in the substance.

The oracle was delivered to us in colored hieroglyphs, to which as yet we have no Rosetta stone. Do these speak of structural, or of chemical, differences in the living substance?

It has been thought they tell of both. Our judgment as to the results in individual cases must undergo revision, possibly suffer reversion.

[2] For do such chemical differences as seem to be registered pertain to the actual living substance; or merely to the substances mingled with it, and forming the environment it creates locally for itself?

[3] Again, may not a seeming chemical difference be, perhaps, merely a difference of accessibility to these substances, grounded on local states, as of viscosity, in a lamellar substance?

[4] And must we, for such states, appeal to final physical, that is, molecular, conditions, or causes; or can we refer them

first to physiological states of the living substance, more within the range of our faculties, and capable of being grouped with, if not interpreted by, phenomena already known to us?

These questions are not gropings far afield; they have not till now been asked from the standpoint of the facts gathered here, but these force them upon us in just this form and through them open up new vistas of research.

[5] Transcending all the difficulties of preservation, was the fact that the protoplasmic structure was found to be in most cases an unstable and often evanescent organization of the elements; and even where a stable structure existed, such as some of those figured for us by Bütschli, this was found to be secondary in importance to swift and subtle substance-changes which it masked.

Transmutations, transitions, permutations, metamorphoses: — all these, in "*fixed*" material can be, at best, but "fixed" states, or appearances, leading to misinterpretation as structural differences, and as such, possible causes even, whereas, in truth, they are registered effects of causes which forever defy fixation.

Special training of the automatic, or registering and will-less, attention was devised and found of great use. I believe these more purely animal faculties, when properly used, will give best results in dealing with such swiftly evanescent phenomena as we must learn in protoplasm; in presence of which a more direct exercise of attention by the will is elliptical, confused, misled, or baffled utterly.

Camera drawing of the finest structure and phenomena I found impossible. Of the living substance-phenomena, it is about as practicable as it would be to trace upon a wall reflections thrown there from disturbed water. Some camera drawings of the filose phenomena in starfish and echinus eggs were made, but such can show by direct tracing larger masses only of the substance, and are in point of time-relation true but to a limited extent. It follows from the very nature of these phenomena, as will be seen, that they cannot be traced. For while the hand follows one minutest portion, the relations of the whole will have undergone change, with important transpositions and transmutations of both structure and substance.

In point of minuteness, also, many of the facts which can be optically noted defy camera tracing, since the finest steel point is still too coarse for the work.

Visible Protoplasmic Structure.

[6] The structure of protoplasm throughout the substance of all living organisms examined, except where secondarily altered, was found to be, as maintained by Bütschli, that of a visco-fluid foam.

This is thought to be amply proven by the following optical appearances:

1. By presence of an optical reticulum, such as described by Bütschli.

2. By presence very commonly, above and below, in proper focal relation to this, of a blistered, or what might be termed a *shagreen-like* appearance, which with inadequate powers looks slightly granular, or uneven.

3. Since in all cases, above or below the shagreen surface, or the network, proper focus yielded a smooth expanse, variably thick, of seemingly homogeneous protoplasm; such expanse being large or small according to the amount of the network in one optical plane at any moment.

4. By presence of protoplasmic films or pellicles intervening between the substance and all contacts involving a viscosity different from its own, whether internal or external to the mass, whether of alien substances or of its own substance.

5. By spontaneous formation of like pellicles freely against all such differences of contact, whenever and wherever they arise.

6. By spontaneous vacuolization taking place in even very viscous areas; also in homogeneous-seeming areas.

7. By similar vacuolization under pressure, or action of reagents; or as marking relaxed states of the substance; and in states heralding, or following, death.

8. Finally it is proven by true protoplastic metamorphoses and activities, not in fluid areas only, but in those which are, as

a whole, very viscid, resistant to pressure, elastic, and even contractile.[1]

The "shagreen" appearance above referred to, when caused by Bütschli's structure, is best seen in peripheral areas, especially where there is a marked alveolar layer; but whether this latter be present or not, the shagreen effect can be strongly marked. It is always to be made out also (if there be no optical interference of substances), where alveoli, many or few, lie in the same plane, or nearly so. The blistered appearance may not come to the surface of pellicles, but lie more or less deep *within* these which vary greatly in thickness; and the actual pellicular surface may be covered more or less unstably by a far finer shagreen, whose alveoli will measure only from one-sixth to one-twelfth μ[2].

Alveolar blistering, whether of the finer froth, or of Bütschli's structure, does not always roughen the actual surface, but may be much flattened; and further, may be covered by a secondary pellicular film; or in other cases may project so as to cause an optical roughening of the surface when seen from the side. I have not, however, in any case yet seen, been able to assure myself that the *actual surface* of any pellicular shagreen, however delicate, as seen from above, was not covered by yet another pellicle.

The smooth expanse of protoplasm found everywhere above and below networks and alveolar contours proves even more conclusively than does the network itself, the presence between inclusions of a lamellar substance. In even swiftly flowing and unstable areas it can be seen forming structureless, or blank, surfaces, which break into fragments the network image, as the flux of the substance carries this above or below focus. The blank spaces are in their turn broken by rounded contours of alveoli rising or falling into focus, and then by reappearance of clearly marked network images.[3]

[1] See Continuous Substance; Activities — filose.

[2] See p. 9.

[3] One may with practice follow for many moments at a time the course of small groups of alveoli, or even of one or two, in the endosarc of amœbæ and other Protozoans, and in the early stages of the development of the starfish and echinus eggs; and while doing so, the true nature of these expanses of "shagreen" texture,

Bütschli has not called attention to these film appearances, but they are very uniformly present, and to be made out with greater or less ease as other conditions may allow. In his figures they are probably to be understood in many places where mere breaks in the optical network are given. In the living substance also, similar breaks in continuity of an optical network are seen constantly, without any other image indicating substance.

[7] Not only is a structure akin to that described and figured by Bütschli found, as he asserts, everywhere in living protoplasm; but the facts go even beyond his assertion; for the substance of his reticulum, that is the "lamellar" and pellicular substance, is found to be itself alveolated; and to have the physical form of a visco-fluid foam.

This secondary structure is most often visible on pellicular surfaces, where it is seen as a delicately blistered, or "shagreen" surface, or as delicate striation lines[1]; yielding at times, with adjusted focus, a network whose meshes are but one-sixth to one-twelfth the diameter, as to alveoli, of those of Bütschli's structure. A pellicle frequently offers room for several layers of such minute alveoli, yet because of their optical smallness, I have not seen in a pellicle, more than one layer.[2] In the meshes proper, the secondary structure sometimes appears as granulation, or vesiculation, or as delicate striation; which there, as well as in the pellicles, may be stable, intermittent, or rhythmical.

The secondary structure is also seen in protoplasmic films, or in extensions from the network of Bütschli, which are, as to their whole mass, less than ½ μ. In such cases there is

or of smooth substance, and of their relation to the network, can be made out clearly. The presence of firmly defined fibres or networks in that plane does not interfere, from any point of view, with these appearances, since the former *lie embedded between the films*, whether these are thick enough to seem smooth, or thin enough to look blistered. Owing to the greater distinctness, optically, of many striæ or fibrils, it is necessary, where such are present to use great caution in focussing for the film appearances. That is, such as belong to another plane of network, for the greater refractiveness common to fibrillar structures may optically interfere if they be above the focus.

[1] See Striation.

[2] See Activities — filose.

often a minute alveolation, which is most unstable as to size and arrangement, instead of the much elongated meshes of Bütschli's structure, which sometimes take its place.

Although an optically linear, hexagonal, or stretched reticulum of Bütschli can be seen in many cases, there are others, and not a few, in which this state of things is preceded by the alveoli being separated from each other by a considerable amount of interalveolar foam; and in place of yielding a true "network" they have a very irregular or subspherical contour. They present, in short, just that difference of appearance which is seen when the bubbles of an ordinary soap-foam are surrounded by a finer froth and are not in direct lamellar contact with other bubbles of their own size.

The local tensions in the fine foam are constantly making the outline of the larger bubbles flatten on this side or on that, or on several sides at once. The whole seeming of such protoplasmic areas is that of an emulsion rather than that of a true foam; but seeing that the interalveolar stuff is itself a foam, and convertible, and converted into the coarser and more regular structure of Bütschli, has led me to call the whole compound a true foam of varied coarseness.

Fig. 1 is a simple, outline diagram of such an area, taken from nature, of the protoplasm of a portion of a starfish egg, before the structure of Bütchli has been more perfected. The smaller vesicles show the finer foam of the ectosarc-like layer, which first forms about the periphery of the mass. In this, also, the network is broader and more irregular than it will be later; and the same general characters of the internal area are repeated.

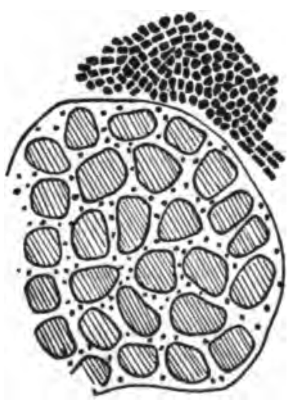

Fig. 1.

The "granules" in such areas are not by any means wholly confined to the nodes of the network but are found, as drawn, scattered through the finer foam.

In the endosarc of Vorticellidæ, and in their cuticular struc-

tures during relaxation, such areas are very common. The most beautiful and regular structure of this sort I have seen was in an immature and unfertilized minnow egg. In the protoplasm of Hydra also exist such areas.

That the appearances, described and figured here, can be explained as an optical illusion, grounded in maladjustment of focus, it is impossible to allow. The actual thickenings of the meshwork, which are common in strial phenomena, are other instances and proofs of the existence of a finer foam between alveoli of the structure of Bütschli, and with powers inadequate to resolve this a greater amount of Continuous Substance than is compatible with acceptance of Bütschli's structure as basic can be readily seen in innumerable cases.

The reader is asked to compare this figure with the drawings in Bütschli's work from preserved material, and even from life, which represent, indeed, veritable and distinct structures of Bütschli as they are formed by natural or artificially forced organization of the elements.

The reticulum, then, is not in all, or even in most, cases a mere structureless film of homogeneous substance between the vesicles of Bütschli's structure; but a compound and highly complex mass of protoplasmic foam, capable of the same phenomena as are areas formed of the structure of Bütschli; which latter is often seen to be directly formed, or evolved, from it by just such changes.[1]

There are protoplasmic structures and organs, and even organisms, whose whole mass is less than that of the interalveolar substance of Bütschli's structure in many cases; and yet within their limits takes place a full series of life activities differing in no essential respect from those characterizing large masses of living substance.

Bütschli himself concedes to the structure associated with his name considerable range in size, — from ½ to 1 μ.

Even in areas where this special structure is marked; and can be readily seen to be characteristic; as in Protozoa, and in early stages of Metazoan embryos, there are intermixed vesicles of

[1] For full evidence of these assertions, the reader must turn to later portions of this paper.

all sizes, all gradations existing between a structure of 1 μ and the fine pellicular structure above described, while transmutations of one set into the other may be readily seen.

On the other hand, there are many areas to be found where the structure of Bütschli is wonderfully perfect and even.

[8] In such areas, as in all others whose substance I have been able to trace from earlier states, I find that Bütschli's structure expresses a secondary and special organization of the distribution of the elements of protoplasm, rather than a final, or intrinsic, arrangement of these.

Kindred organization of the elements is seen in the Protozoa everywhere, heralding, and indeed making possible, areal specialization and areal organization of physiological function; and in the development of Metazoan embryos, the larval and embryonic physiological areas, or organs, were seen to be laid down in the same way.[1]

[9] To sum up: Bütschli's structure, that is, the vesiculation of ½ to 1 μ, is the true structure of protoplasm in so far only as it is a characteristic arrangement of the elements in the form of a viscous, foam-like, emulsion.

[10] The secondary finer structures of the meshwork substance, taken in connection with certain activities of this, to be described further on, seem to place beyond dispute, that the structure of ½ to 1 μ, is not, indeed, the final structure of the living substance, but that it is part only of an infinitely graded series of vesiculations of the protoplasmic foam; whose minuteness it would be rash to limit even to the finest pellicular network visible; and whose coarseness it would be still more arbitrary to limit by one μ.

These facts were established during research upon the following organisms: Amœba proteus, Amœba radiosa; Actinophrys sol; Actinosphærium Eichornii; Raphidiophrys, of several unidentified species; Monads of numerous sorts; Choano-Flagellates of several species; Vorticellidæ in several families, notably Epistylis; Myxomycete found in salt water, Myxomycete found in fresh water; Stentor; Acinetans; Coleps hirtus; and many

[1] See Areal Differentiation, and Striation.

other forms of the Protozoa which crossed the path of my work from time to time, and were used passingly as corroborative evidence; Hydra viridis and Hydra fusca; Turbellarians; Anguillulidæ; Rotiferæ, adult and embryo; Starfish and Echinus embryos and larvæ; frogs' eggs; fish eggs; tadpole's tissues; crabs' tissues and the Leucocytes of crabs' blood; also many fresh-water Crustacea; fresh sciatic muscle of the dog. In plants, Spirogyra, Chara, Nitella.

Composition of the Protoplasmic Foam.

The protoplasmic froth is infinitely complex in character of its constituents, and in arrangement and grouping of these, which, in Metazoa as well as in Protozoa, are subject to more or less gradual change of size, and of actual, as well as relative, position.

[11] A substance formulated as a visco-fluid foam must have its elements, however multiple their character, divided at any given moment into two broad physical groups. This is the state of things we find characterizing protoplasm.

There is first the element, be its nature simple or complex, which forms at any given moment the lamellar, or enclosing substance, of the foam vesicles, throughout the whole or any part of the series of structural subdivisions.

This is, physically, the Continuous Substance.

Secondly, we have those elements seen as the substances included in the vacuoles, or cavities, of the foam: these are isolated to some extent from each other by lamellar films; and in each structural series by interalveolar material, which in different masses or areas, or in the same areas from moment to moment, varies in thickness, in constitution, and structure, as well as in quality, or viscidity.

The substances so isolated are, therefore, at any given moment the Inclusions, or the Discontinuous Substances.

Where the continuous, or interalveolar substance, is itself a compound emulsive froth, repeating the characters of the whole mass, it is true the two groups of elements, from the standpoint of Bütschli's structure, may seem to be in a sense almost inex-

tricably mingled; yet for the physicist they remain clearly distinguishable at any given moment.

That this is true for the physiologist also will be presently shown.

DISCONTINUOUS ELEMENTS OR INCLUSIONS.

In character these are most heterogeneous. They may be subdivided into Simple and Compound inclusions. They are fluids, of various degrees of viscidity, with or without suspended substances[1]; or solids; they may be concretions, or secretions, or excretions; native or adventitious.

Even very small areas are found to contain many chemically different inclusions.

Under Simple Inclusions are grouped the alveolar contents of Bütschli's structure, or of the finer froth, or of coarser alveolation; wherever no interpenetration of the continuous element, subdividing the mass into a finer froth can directly or indirectly be detected. Simple inclusions may be of one substance, or of a number of mechanically mingled substances. They are sometimes transformed into members of the second group by activities of the lamellar substance.[2]

Under the head of Compound Inclusions are placed those areas, *irrespective of both actual and relative size*, where are grouped together alveoli, containing, as far as can be optically or chemically demonstrated, the same, or very similar, discontinuous substances.

The lamellar substance of these inclusions unites to form one common pellicle which, with or without modification of various sorts, separates them as a mass from adjacent protoplasm. Such groups may be built up on a basis of the finer froth; and then form one or more inclusions of Bütschli's structure; or they may be built up of the latter only, or of both; but in all cases the mass is an aggregate of single vesicles, and therefore interpenetrated at some time, if not always, by the continuous substance, which when visible forms an optical network.

[1] The Protozoa furnish endless instances of mingled inclusions.
[2] See p. 19.

Some compound inclusions have become very familiar to us under the names of starch, yolk, pigment, the "granules" of the network; and chromatin, as fibres, granules, masses, or networks.

Yet even of these long-known substances much remains to be learned. Many questions that now leap into almost imperative urgency have, up to this time, scarcely shaped themselves.

Which of these substances are stimuli; which are food for the final protoplasm; which are excretions, which secretions; which are means to an end; which attained ends? In other words, which are final, which intermediate, agents in producing the physiological results we can trace?

Such questions are puzzling enough when applied to the elements of the structure of Bütschli. More puzzling still must it be to answer which of our results, in any given area, are due to the inclusions of this alone; which to the interalveolar substance, with its inclusions. And finally, may not some of the results had in the inclusions of the structure of Bütschli, be due to secretions or excretions of the interalveolar substance under irritation?

The substance called *yolk* seems to me one of the most interesting problems. When one considers that in cases such as are met with in certain rotifers, the whole of a huge ovary, containing material for a score of eggs, is converted, under certain conditions, into a single egg; and that nuclei, as well as the already prepared yolk, go to form the "yolk" for this monster egg: the question naturally arises; which part of the whole mass of intermingled material goes to make up the organism which issues forth in the following spring?

We know that yolk disappears largely, if not wholly, during process of development of the immature creature. But let me emphasize here what all the facts collected are ceaselessly emphasizing: that optical disappearance, under such conditions as exist in the protoplasmic froth, may mean several widely distinct sets of phenomena.

Given the finer structure of the interalveolar substance, many obscure phenomena associated with the life history of all these substances become more intelligible.

The structure and growth of starch grains, and possibly the behavior of their different layers in swelling; the froth-like structure which no treatment seems to take from them; the redistribution at times of their substance through the protoplasm; the formation and dissolution of yolk, which in some cases at least, is a physical process before it seemingly becomes a chemical process; the numerous redistributions seen to take place in the nuclear element we call chromatin: — all these become intelligible if interpreted as phenomena of the finer froth; differing in point of minuteness only from characteristic phenomena seen in Bütschli's structure.

Such an interpretation is not only plausible but is forced upon us in many cases by the optical phenomena attending the physical fact. It is indeed hardly to be escaped, for down to the limits of vision there is found in all parts of living masses a certain absolute unity of structure and of phenomena.[1]

[12] Similar evidences that the *network "granules"* are of the nature of compound inclusions, are to be had in their disappearance during structural reductions, or subdivisions of Bütschli's structure, which produce an appearance of homogeneous protoplasm; and in their reappearance upon return of the structure to the first coarser organization which produced a distinct network.

[13] The universal presence of the "granules," or of the element which is so named, as seen in Bütschli's network, suggests that we have here an element, which is in some way essential to some if not all of the characteristic activities of the substance; that in the form in which it is best known it stands not merely for a passive chemical inclusion, but for a physiological area or substance organ.[2]

Certain strong resemblances of the granules to the *chromatin* of nuclear threads may be not wholly superficial, but hold the clue to a right interpretation of these most interesting substances.[3]

How long the lamellar substance of compound inclusions persists in a living state, and what, during that time, may be

[1] See Areal Differentiation; also Activities — filose.

[2] Idem; also Habit.

[3] For movements of the granules, see Activities — filose.

its relations with the surrounding protoplasm; whether, unlike the major part of the network stuff, it is stable in position; or like this, in constant flux of intercourse with surrounding areas; whether the inclusions are in constant use by the substance; or whether they are simply storehouses of chemical influence, withheld for special times or crises in the life-rhythms of the mass, or portions of it: — all these questions now present themselves as to the substances distinguished in Bütschli's structure; and we need the answer.

Inclusions may also be subdivided into *microscopic* and *macroscopic*. *Microscopic*, are those which lie within the lamellar alveoli of Bütschli's structure, or of the finer froth; *macroscopic*, those which are built up of these, forming, in any living mass, areas, or structures, relatively large.

[14] When dealing with the living substance strictly as such, and with organisms as masses of protoplasmic foam; all endo-skeletons, all vascular systems, all body cavities, have for the substance, or the mass, the same value in a physical sense as the alveolar inclusions have for the lamellar substance.

Even exo-skeletons arise in many cases as protoplasmic inclusions, and later, by withdrawal, or atrophy, of the living substance, become more strictly external.

It is interesting that this statement, in at least one instance, can be applied to the membrane of plants also. The cellulose wall of very young Spirogyra filaments was seen to be covered by a most delicate film of living substance, of which the alveoli were hardly one-sixth the size of alveoli of Bütschli's structure. They were elongated and arranged in parallel rows. Most curious of all was it that the rows of alveoli followed with perfect sympathy the direction of the internal spirally twisted chlorophyll bands, so that the surface under a lower power appeared most delicately striated longitudinally; as if there were in the nature of the whole plant substance the same spiral tendencies. The inclusions appeared to be homogeneously fluid. In older specimens this outer film disappears; either obliterated by the increasing deposits of cellulose, or having itself migrated to the interior of the cell. The

cellulose wall of Spirogyra, then, exists at first as a substance inclusion.[1]

Throughout the series of structural subdivisions of protoplasm the inclusions are for the most part unstable. They are seen to increase either slowly or rapidly by purely physical changes; and they suffer change also by what must still be called *physiological* activities of the interalveolar protoplasm. They grow by absorption of material from, or through, the surrounding substance; they wane by diffusion in the same mode; they are at times suddenly augmented by relaxed states of the nearest interalveolar stuff, or of the whole area, or mass, and may then attain such size as to rank with "vacuolations"; or, from a size too small to be directly seen as alveoli, may be brought into the range of the structure of Bütschli.

Inclusions may be also more or less rapidly increased in size by withdrawal of the interalveolar substance, which involves, or leads to bursting of, the lamellae; throwing together the contents of adjoining alveoli. Besides a purely physical cause of this sort, such as is familiar in soap-foams, there are cases in which the interalveolar, if not the lamellar, substance *crawls or flows away from between alveoli.* This phenomenon has been seen in many Protozoa; typical instances are readily watched in Heliozoa, as Actinosphærium. In the formation by these of tubular rays, and by Acinetans of hollow tubes or suctorial tentacles, there can be little doubt as to the way in which the transfer of protoplasm takes place.[2]

In Acinetans there is formed a rod-like extension of the substance, which by successive redistributions of the elements becomes at last a mere row of alveoli of about equal size. The network of the whole has the effect of a "ladder," whose sides are increasingly thickened by immigration of protoplasm from the "rounds." These latter are finally obliterated as a result of this, and the whole interior is then one long closed

[1] It is not impossible that to contractions of such a film of organized protoplasm may be due the movements of many plant filaments, as Oscillatoria, etc. See Striation.

[2] Each one of these phenomena, it must be remembered, can be fully grasped only by aid of all the facts given in this paper, which are supported by hundreds not given. For above, see also Activities of the Continuous Substance.

tube full of fluid which has a pinkish tint. By similar activities the end of the tube becomes very much thinned, and at last bursts open, much as a bubble would, in the centre. The protoplasm then moulds itself about the rim and the tentacle is ready for use. The whole process occupies a few moments.

This is one of numberless instances, which go to show that it is the interalveolar rather than the inclusion substance of protoplasmic foams, which is the living substance.

Fluid alveoli of Bütschli's structure are subdivided in a number of ways. They have been seen to be *constricted, or pinched, in two,* precisely as large vacuoles are at times. This occurs in the endosarc of amœbæ; in the formation of ectosarcal parts and organs, and in other reorganizations of the elements. They are broken up also by what appears to be a relaxation of their lamellar substance, at the same time with the surrounding substance; for this latter at such times seems to lose in viscidity and to become more or less mechanically vacuolated.

They are at times penetrated by filose processes spun into their interior from the interalveolar substance. Whether the actual lamellar substance takes any active part in these processes could not of course be optically determined. In the endosarc of Amœbæ, where the phenomena were first observed, the simple filose processes were seen to branch. In the Vorticellid, *Epistylis* — in the somewhat larger alveoli of whose cuticle the same thing was later seen — the simple filose extensions were swiftly ramified, until a distinct network was formed. From this, in some cases, a finer froth appeared to be formed later, in what manner could only be conjectured. The filose processes may spin quite across the alveolus and become fused with the opposite wall, or return to the main thread, or the wall whence they came. The process is best described by likening it to characteristic activities of the Protoplast *Gromia.*

It is not impossible that there may exist already in the fluid inclusion a fine network, invisible by reason of the tenuity of the lamellar substance, and that the filose processes merely follow the course of the lamellæ, pushing between the yielding vesicles very readily, by reason of a rather greater amount of

viscidity. That the filose formations were *free is not, on the other hand, at all less likely*, as will appear under Protoplasmic Activities. The phenomena were seen to take place while the general cuticle, as well as the whole mass of the animal, was quite strongly contracted.

[15] This proved that under the mask of a stable and even a contracted area of Bütschli's structure, local relaxations may exist, rendering possible not only transfer of substance but modification of the finer structure of the living substance. It also went to show that of the two groups of elements it is not the alveolar contents which play the leading rôle.[1]

Variations of size of alveoli in correlation with physiological function will be discussed further on.[2]

[16] There are found in the living substance innumerable contradictions of the conditions ruling the artificial foams of Bütschli. Many of these are to be cited. It may be stated here that as to size and distribution of inclusions, as in most other particulars, while there are always cases to be met with which coincide with the inorganic foams, there are more which cannot be made to agree.

An adequate explanation of living phenomena must meet all the facts.

Such intermingling of various matters as exists in protoplasm must render chemical analysis of this, *as living substance*, forever difficult, for besides the fact that the two sets of elements are so finely subdivided and so intermixed in very small portions, — portions so small indeed as to pass at times beyond microscopical vision,[3] — how shall it be determined which part of the result belongs to which group? In our efforts to learn something of the actual living substance, how shall we know which part of a given reaction, or which among all the detected qualities or matter, belong indeed to the living element; which to the intermingled and non-living matter? How may we know, which part of local or temporary variations are due to local variations in these latter; which to physiological difference in the functioning

[1] See Activities — filose. Also Striation.
[2] See Areal Differentiation — Ectosarc.
[3] See Living Substance as Such.

substance? And finally, which part of the constant results is constant as living substance; which but as its environment?

A still more radical question has not yet been disposed of: how are we to know that there is in the whole compound anything more than interaction, under physical controls, born of their physical arrangement; of non-living, of chemical materials?

All of these questions, not excluding the last, have received for me illumination from study of the inclusions of living protoplasm; and yet more light from study of the continuous substance. Though not answered, they receive limitation which may later help us to an answer.

Nothing is more common in protoplasm than an areal organization, more or less unstable, of the vital phenomena, so that such areas are traversed by the same special phenomena, and the whole may be called physiologically homogeneous throughout. Yet in such area of organized physiological function, the inclusions of Bütschli may or may not show homogeneity in kind or size, but may be thoroughly heterogeneous.[1]

While this is possibly explicable by supposing homogeneousness in character of the finer froth inclusions, this is but to emphasize the answer already indicated; and further, to show that not only must we not look to the inclusions of Bütschli's structure for the basis of such homogeneity of function; but that we shall find it in the interalveolar stuff.

A sensitively organized activity, and reaction to stimuli, throughout an area whose inclusions are mingled solids and fluids, and of all sizes, may hardly be interpreted as physical interaction between a homogeneous lamellar substance and such chemical and physical heterogeneity. Neither diffusion nor surface tension can readily be brought into play here. On the other hand, the continuous substance in such areas, as in all others where organized physiological activities are found, has definite and most homogeneous characters.

[17] In the section on contractility it will be shown that in this most important activity, so far as all optical evidence goes, the alveolar contents form the passive group of elements,

[1] See Striation — fibrillar.

responsive by change of shape or relative position to compulsion of interalveolar activities; while the network substance, down to its most minute subdivision, shows a true, characteristic rhythm of shape and position.[1]

[18] It is the mode of distribution and optical characters of the continuous substance, as well as certain constant changes that take place in these, which further make it certain that in the structure of Bütschli, and beyond this to the limit of vision, and again beyond this, it is the continuous substance which manifests the characteristic activities of the substance, protoplasm.

[19] To sum up: there was found no optical evidence in any material examined, to show that the part played by the discontinuous substances is anything more than a passive chemical and physical rôle; while there was endless and ever unfolding evidence that it is the continuous substance, at any given moment, which sustains the rôle of the living protoplasm; and as far down in the scale as the human eye with its most powerful aids can trace it, it is this same continuous substance which we must be content yet awhile to call the living, the physiologically active, stuff.

CONTINUOUS, OR LIVING, ELEMENT.

In dealing with the continuous element it becomes necessary, in view of its compound nature, to subdivide verbally what has hitherto been spoken of as Bütschli's lamellar substance, or Bütschli's network. It is necessary to distinguish in various cases the whole continuous substance of the physicist, which includes in a given structure both alveolar lamellæ and the interalveolar foam; from the latter as a thing by itself. This is the more forced upon us since we must now learn to think of optical networks and lines as by no means identical with those actual fibrils and networks whose existence is shortly to receive proof.

The word "network," as commonly used, brings with it an element of confusion, in that it does not clearly distinguish

[1] See Striation and Contractility.

between actual lines and included spaces. Further "network" ill expresses a structure existing in three dimensions of space.

I shall therefore restrict the use of this word to the optical network effect, whether this at the moment expresses a physical fact or an optical figure; and also, when not otherwise specified, to mean the intersecting *lines* of this, excluding interspaces.

By *continuous substance* will be meant the whole substance separating inclusions — that is, it will be used in the strict physical sense.

Interalveolar stuff, or material or foam, or substance, or protoplasm, will be used for the continuous substance, *exclusive of the actual alveolar lamellæ:* and *interalveolar structure,* as descriptive of the distribution of the two sets of elements in this material.

By this phraseology, which will presently be seen to be very necessarily precise, many mental difficulties and much vagueness are evaded in dealing with protoplasmic foams.

CONTINUOUS SUBSTANCE.

Our conception of the lamellar substance of Bütschli's structure being enlarged by knowledge of the finer froth structure within it, we must now image to ourselves the true continuous substance as forming the lamellar and also interalveolar stuff of the finer foam ; then, as being continuous by way of these with the lamellæ and interalveolar stuff of Bütschli's structure; then, by way of these, continuous with all pellicles internal to the mass ; and finally, in the same manner, continuous with the external, or mass, pellicle and its products.

This state of things can be seen in many transparent areas, and in some entire masses of protoplasm. Those optical appearances, upon which objection to the fluid foam structure of protoplasm has been based, such as fibrils and networks of indubitable firmness, are here for the moment set aside, as, though their existence will later be finally proven, they will also be shown to be coexistent with, and in no sense inhibitive of, a true foam state.

[20] In one respect the kinship between protoplasm and artificial foams, as established by Bütschli's masterly researches, holds good and is not to be shaken. As to the formation of pellicles, the physical nature of the substance seems to rule, and never, so far as I have seen, is it set aside by those controls which elsewhere appear to dominate from time to time that physical mastership of the elements Bütschli has demonstrated.

This fact, as pointed out above, is one of the strongest evidences of the true nature of the substance.

From mass pellicles in all their varieties,[1] through the series of inclusion pellicles down to alveolar lamellæ and pellicles of the finer foam inclusions; the living substance maintains its habit of surrounding all physical differences of contact with a continuous film of its own material.

But this basic unity of structural form covers an infinity of structural differences, of which many organisms; not less those which for many years biologists have termed "simple," than members of the highest groups; will furnish abundant proof.

Only the most obvious of these have so far been noted: vast fields for research are now seen to open out in respect to those which are not only less conspicuous but also in many instances more evanescent organizations of the elements.

In an amœba, for instance, the peripheral pellicle which stands for cell wall, the ectosarc possibly, the contractile vacuole, the food sacs, the nucleus; — these have been taken to be the limit of organization of the substance in this lump of "primitive protoplasm."

So far as these well-known areas of differentiation of the living substance go, they were seen, with respect to the foam structure, to be optically separated from each other by character of their inclusions and of the continuous element; and by the mode of distribution of these two in relation to each other, not only as permanent differences but as differences from moment to moment.

Besides the broad areal differences noted, there exist local differentiations more or less unstable, to the point of such evanescence often as makes it difficult to catch a glimpse of

[1] See also Ectosarc.

their fleeting existence. ***But none the less are they areal differentiations of structure; and none the less are they associated with physiological function of the substance.***

In Metazoan eggs, as of starfish, echinus, rotifer, fish, or frog, in Metazoan larvæ even, the same holds equally true.

It may be said for living protoplasm, that of making pellicles there is no end. Yet the pellicles when made differ one from the other as markedly as, in many cases, do nuclei, or cell membranes, or skeletons, or any other coarser, complex structure of the substance.

The optical network of Bütschli's structure is found in all protoplasmic masses I have seen, to be locally emphasized so as to form optically greater separation between areas of the substance by marked partition lines, plates, or membrane-like thickenings of the lamellar film.

Such modifications are to be grouped, both in structure and origin, with the pellicles surrounding external masses and forming contact surfaces.

Like these, they are actual thickenings of interalveolar stuff along lines of the physical lamellæ, and mean that here the mass of interalveolar foam has been augmented, or has undergone physical modification of some sort.

We must now begin to distinguish verbally between the necessary physical, or purely physical, pellicle and such thickenings as these. For the former I shall say physical pellicle, or lamellar substance; for the latter merely pellicle, or pellicular plate, thickening, or membrane.

[21] Wherever a finer foam structure can, directly or indirectly, be traced in a pellicle, it follows, from the nature of the case, that the outer surface of that pellicle is in its turn covered by a pellicle. Hence, wherever pellicles are augmented by interalveolar material they are double; and actual contact with environment, whether this be internal, or external, to the mass, is made by the pellicle of the finer froth.

Fine instances of this are seen in the pellicular formations of Vorticellidæ.

Because of phenomena found associated with flux of pellicular substance, it becomes impossible to set a limit to such

multiplication of pellicles, even to the end of microscopic vision.[1]

[22] Pellicles differ one from the other, or at different moments of time, from their own former states; in point of thickness, of viscidity, of finer structure, and of stability in the component protoplasm, as well as in activities of this. The same is true of the interalveolar substance throughout its formations.

The varying viscosity of pellicles is shown by optical increase of density, which also brings a characteristic change of hue; and by change of refractive value; with increased resistance to pressure and increased elasticity. At such times, owing to these optical qualities, structures so minute, or expanses of substance so tenuous, as to be in more fluid states wholly invisible, become readily detected.[2]

It has been urged that to be capable of contraction, protoplasm must needs be a solid substance; it has also been affirmed that if a fluid it cannot be *elastic* as contractile substances are.

That both of these conditions are fulfilled by the substance and that it yet does not for these renounce its typical fluidity can be proven by hundreds of instances. A single instance will suffice to make this clear.

The pellicle of the contractile vacuole of amœba, which is at times so fluid as to mix freely with the surrounding protoplasm, becomes at other moments, notably while in that very viscid refractive state which rhythmically precedes the collapse of the organ; so very firm and so truly elastic that the vacuole suffers constant change of shape under pressure of the endosarc, of the included substances also, and the peri-neuclear area, if present. At such times it looks most like a transparent rubber bag filled with water.

Conversely, the instant return of a most elastic and highly organized area to a truly fluid state is beautifully shown, when, by breaking or tearing tension, the stalk of a retractile vorticellid is torn apart. Then the contractile muscular fibre, which

[1] See Activities — filose; also Substance as Such, description of Choano-Flagellata.

[2] See Striation.

is composed of a number of different areas, suddenly rounds itself off and shows a smooth surface at the broken ends, while at the same time the different areas fuse smoothly together at this region and can no longer be distinguished apart. The same experiment can be tried in higher muscular areas, as of rotifers.

In relaxed states, areas of the structure of Bütschli which were before very viscid, become so fluid in seeming with respect to that structure, that the protoplasm presents the appearance of mixing freely with water. So with the finer structure; states of such viscidity as caused elasticity of the continuous or interalveolar element, may be followed by relaxed states in which the protoplasm proper of Bütschli's structure seems miscible with water.

Such appearances as described above may characterize the whole of a pellicular area or be distributed in lines or networks within it, at varying distances from the surface. In these latter forms, they furnish, at times, the only direct evidence of alveolar structure; and they then prove also that there is organization of the elements for physiological function.[1]

Upon formation of physical pellicles where the area of contact, internal or external, involves a number of alveoli, there seems to be a tendency in protoplasm to thicken the film so formed by access of interalveolar material.

In a similar manner, that is, by interalveolar material and outflow of what has been termed hyaloplasm from the endosarc, ectosarc is formed. Almost all pellicles, certainly all those of Bütschli's structure, are in strict sense an ectosarcal formation, no matter what position they hold in the mass.

The viscosity of the continuous substance varies locally from moment to moment, the changes being often miraculously swift. From a very fluid state it will become rapidly so viscous as to resist pressure after the manner of a stiff elastic bristle; and this may take place without change in size of the visible foam structure.

In such states it is as a rule markedly contractile; and commonly the assumption of organized contractile activities by an

[1] See Striation.

area can be foretold by just these characteristic differences, which are identical with those seen in most ectosarcal areas and products.

It is by local differences in viscosity that differences of shape in masses, which had their origin in protoplasmic activities, are maintained, until they may or may not be released to pass into physical control of secreted, or adventitious, non-living materials. The same is true of those internal cavities, or vesicles, whose complex, non-spherical forms have been used as an argument against Bütschli's foam theory.

Variations in viscidity of the substance as masses, or areas, are optically manifest as differences in the same manner as shown for pellicular substance.

Increased viscidity does not always mean structural subdivision of Bütschli's structure, although this of itself is physically a common cause of increased viscidity (*ceteris paribus*) wherever it occurs.

Nor does it necessarily mean in living foams, as it usually does in physical foams, an increased tenuity of the lamellar membranes of Bütschli's or other visible structure.

In living foams, the structure of a given area of great viscidity may be in size not at all different from surrounding areas; yet the viscidity shown under pressure, or osmotic conditions, may be far above that of these latter.

The continuous substance may be no thinner, may even be markedly thicker, than that of the adjacent protoplasm, and yet the areal viscidity vastly greater.

Hence comes it, that there is often found an areal viscidity which may have almost any structural character in point of size of alveoli, or distribution of the continuous element of a given structure.

All such states and conditions may be seen freely interchanged and playing freely into each other in the protoplast, *Amœba radiosa;* coarse and fluid structure changing in a moment's time into minute and highly refractive areas; these returning to coarse and highly viscid states; these again to finely subdivided states, which may be either fluid or viscid.

At one moment the substance becomes a film so tenuous as almost and then quite to elude the most careful search, yet having a true structure of Bütschli; then gathers itself up into blunt pseudopodia of great thickness, and of double, or triple, or manifold, alveolar differentiation; then spins itself out into long delicate whip-lashes, which are at first coarsely structured near their bases, but pass into invisibly subdivided states, and become so viscid as to bend under mechanical pressure of the cover-glass, like a stiff bristle as they extend straight out in the water. The tip of these rays may elongate still further till a fine thread forms. Before, or after, this last change they are optically so refractive that they glitter, and have a greenish hue like glass rods.

In pseudopodia so modified, are seen contractile activities; for they bend about like tactile organs, as, indeed, they prove themselves in various ways to be for the time. At other moments they bend their length into contorted spirals and ram's-horn-like shapes, and then again, lengthening, will lash the water about in a frenzied way exactly like overgrown cilia or flagella.

A momentary touch upon the cover-glass will in one moment convert all of this display into inactivity, leaving but a shapeless lump of slightly amœboid protoplasm, which usually sinks more or less in the water. That area in the mass from whence arose the contractile processes is different for a few moments, has a more uneven and disturbed appearance than the rest of the lump. And when the creature resumes its activities, it is from this same area that there usually arise again new organs having the same peculiar characters and showing the same metamorphoses and activities; while those portions whose processes were more ordinary pseudopodia again produce these; showing that the activities, though intermitted, were only suspended, and that their suspension was a phenomenon physiological, and not of physical control alone.

It must be remembered that the slight jar to the cover-glass was only one of countless vibration disturbances to which the animal is subjected; of a different character from those occasioned by passing organisms, but still only a jar, which

seems from a physical standpoint inadequate to cause such transformation, unless, indeed, it were sufficiently disintegrating to prevent renewed manifestations.

In the vibratile state of the processes, delicate transverse striations could fleetingly be seen in their lower portions. Delicate, cilia-like, appendages were at times produced from very blunt ends of other lobose pseudopodia in this form, and were also vibratile, and acted as tactile organs.

To the student of the substance, this form is recommended as uniquely fruitful.

[23] In all the above facts, areal viscidity of the living substance was seen to be something independent of the physical distribution of the elements in any given, visible, structure, especially if that structure were Bütschli's.

[24] It is worthy of special note that in some viscid states, which show increased elasticity, or even mere increase of refraction, pellicles resist longer the passage through them of hardening, killing, or even staining, reagents. Their kinship with ectosarcal formations is by this more fully established. The same property characterized the interalveolar stuff wherever found in a similar state. Unstable interalveolar formations having this quality persisted also in preserved material as distinct substance structures, and then had every appearance of those substance structures which are more stable in life.

These facts offer a valuable hint as to a possible cause of such structures as "achromatic protoplasm," or "archoplasm," in eggs; and as to differing results given by preservation methods in nuclear and cytoplasmic phenomena at different times in the rhythms of cell division phenomena.

I find that where very viscous states of the interalveolar material caused viscid states of masses, the latter were relatively difficult to stain; and, unless the viscid stuff had the limited physical course of fibres or networks, it was less easy than usual to kill, stain, or fix quickly the areas enclosed or cut off by it.

In developing starfish and echinus eggs, there are rhythms in amount of time required for stains, or fixing reagents, to act, and these are sympathetic with rhythms of resistance

to pressure, of the whole eggs, or of the peripheral areas. The same held true of internal areas, which had rhythms of resistance, and at the same time showed like variation in resistance to pressure.[1]

If we simply throw eggs into some killing and hardening material, and wait for them to be dead enough, and hard enough, to resist the severe strain of subsequent operation, we necessarily miss much information from the substance as to how it is affected; and how it reacts to the treatment.

It seems to me such use of reagents should also be considered in the light of inducing pathological conditions; that the chemicals used should be watched *as modifiers of the living substance, — as drugs, in short.* It is not impossible the science of medicine may thereby be indirectly aided. (See Selection of Environment.)

[25] Most remarkable of all physiological peculiarities correlated with areas which are marked by stable or rhythmic viscosity of the substance, as associated with organization of its elements; is an increased tenacity of life under adverse conditions.

[26] I find that when an organism is crushed, or dissected, the power of continued existence is shown most specially by two groups of substance structures, whether the creature be Metazoan, or Protozoan:

In the Protozoan, those portions which at all or most times maintain protoplastic activities, notably those which are filose; and those portions which show marked organization of the elements for contractile activities:

Those portions of the Metazoan which at all or most times maintain protoplastic activities as their characteristic activity; and those areas which show marked organization for contractile activities.

When an aquatic Metazoan is crushed, the muscular tissues are the last to die, — that is, to become vacuolated, and to have disorganization of the elements set in.

The same is true of all aquatic Protozoa and the few endoparasites I have examined.

[1] See also Activities; — rhythms of viscosity in starfish eggs.

[27] And of all such structure in both classes of animals, modifications of the finer structure for contractile activity as in filose masses and pellicles, persist longest in an active state.

Of higher forms, I have to offer as evidence in this connection only such as is given by the crab and the frog. In the first class of structures cited, the protoplastic areas, the retention of primitive powers of local adaptation to environmental conditions, such as the lowest forms of the substance possess, which include a marked power of swift and stable organization of the elements, and of swiftly varying the viscosity of the interalveolar stuff; evidently serves to maintain in such areas a physiological existence, independent of the organism which *in toto* is the food provider for all areas. The limit of existence of such areas must be to great extent the limit of the stored up food, or stimuli, represented by their inclusions.

In this connection it is hardly possible not to refer to the strange vitality and power of independent existence shown by those curious substance structures, the leucocytes of crab's blood. These, five hours after being drawn from the animal's body while it was in the soft-shelled state, still actively formed colonies, and exhibited free protoplastic phenomena. After general connection of the cells had been established throughout the whole by filose processes spun out to excessive delicacy, there was a marked effort on the part of those nearer the periphery to spread themselves out in quite a special way, in flat, almost parallel processes, which again spread themselves out laterally, so as to form sheets and webs and mats of protoplasm; producing at last a covering, or envelope, of very viscid substance for the whole. A good deal of *migration of the individual cells* was involved in these activities. The envelope had for the unaided eye a viscid, gelatine-like appearance, and when placed in strong light refracted from the surface. It was at the end of two hours so viscid and firm over the surface of a small wine-glassful of the blood as to sustain considerable pressure.

The whole mass had now the value of a mass of protoplasm, or even an organism, for the filose processes everywhere bound the once single units into a firm union. The fluid surrounding them had the value, as to the external pellicle, of a mixed in-

clusion, interpenetrated by filose processes; while the external layer had the value alike of ectosarc, and of a pellicle or pellicular membrane.

Those leucocytes whose first position was nearer the center of the mass, behaved quite differently from those of the periphery. They coalesced changefully into ever-increasing lumps and masses of protoplasm, spinning threads and webs in all directions, even to the very periphery where they joined themselves to those units forming the membrane.

There seemed to be shown here an organized effort on the part of members of the artificially formed colony to make an *inclusion* of the serum, and so to retain for the common substance its accustomed environment as long as possible. (See Selection of Environment.)

In the second class of structures, cited above as having persistent vitality; the inclusions being already of an organized homogeneity in character, the power of the substance to vary local viscosity, and to maintain it, is thus emphasized, and necessary local food, or stimulus, is better conserved and controlled.

In preparation for encysted states an envelope of increased viscosity is first formed; sometimes there is merely increased viscosity of the pellicular membrane of the organism; sometimes a separate membrane is formed by exudation, or possibly spinning phenomena, but this latter in these cases I have not seen. Echinus eggs were seen to form membranes by filose phenomena of the pellicular stuff.

The breaking up of the original mass of a Protozoan into swarm-spores, or into macrospores, is possibly another mode of using a more viscous and finely organized state of the elements for preservation of the substance; for these products are always surrounded by a very viscous and finely structured area, and, moreover, are supplied with motile appendages which are also tactile and prehensile, *by whose means the substance seeks a new and more favorable environment for itself.*

[28] I have observed in all *young* of Protozoa a markedly greater resistance to adverse environmental conditions; a tem-

perature or state of the water which had caused death to the adult mass as such, seeming for these innocuous. Where death was escaped by the adult through formation of macrospores, these reorganizations of the adult mass showed an indifference to adverse conditions which was in many cases remarkable. I have seen Protozoa spores swim actively for many minutes in strong solutions of poison, such as corrosive sublimate, and to resist for some moments ammonia, the faintest trace of which actually disintegrated the adult.

These facts may go to explain partially the extraordinary resistance of bacteria and their spores to action of heat, cold, and other states inimical to the living substance.

The prevalence of egg membranes and of ectosarc-like areas in embryonic states of Metazoan substance also receive here some light.

[29] It was found that to shake starfish or echinus eggs, in early stages, not too hard, was productive of perceptibly greater resistance to reagents, to shaking and also to pressure; in other words, the viscosity of the mass, or most likely of the peripheral portion, was increased by such treatment. The same result was had from pressure, not strong enough to rupture, between cover and slide. The substance here opposes an adverse environmental condition by a physical change of state. In this connection there are facts obtained in the study of contraction phenomena which are of vital importance. The reader is most particularly referred to the phenomena of cell-connection, both as seen in mechanical experiment and in the natural course of events.[1]

An excellent instance of rhythmic variation of viscosity is had in the pellicular membrane which forms the wall of the contractile vacuole of amœbæ. This was found, contrary to the most widely accepted belief, to be not a stable, or persistent, substance structure. The subjects of observation were *A. proteus* and *A. radiosa.*

At times in its rhythm, though not in each recurrence of this, the vacuole disappears; not merely optically, but actually. For during collapse, which at some times seems to be more

[1] See Activities; — rhythms of viscosity.

complete than at others, the pellicular substance becomes so completely relaxed, so fluid, that it mingles with the interalveolar substance of the surrounding protoplasm, and the vesicles which at one time in the rhythm formed a more or less perfect alveolar layer about the swollen vacuole, are also mingled freely amongst those of the surrounding substance, after the manner of endosarc. As the membrane re-forms after such collapse, its thickness, which at first is slight, is gradually augmented by access of interalveolar stuff; and at the same time it undergoes more or less modification of its optical qualities, until near the most distended moments of the vacuole these qualities are at their maximum. That obliteration of the membrane is here a physical fact, and not mere optical illusion, is shown by the flux of the vesicles amongst each other, and also by the failure of even osmic fumes at such times to show a trace of substance modification, about the point of collapse; while, on the other hand, during ordinary collapses, when the pellicle becomes merely plicated and difficult to detect optically, one can so preserve a very definite substance structure.

Nor is the vacuole itself a permanent organ in the strictest sense, since, contrary to the accepted idea, it does not persist at one spot in the endosarc throughout the life history of the animal, but as I have witnessed, may fail after collapse to reappear where it has done so for hundreds of consecutive times. When this perhaps rare phenomenon occurs, the protoplasm of the immediate area has a very fluid, *vague*, appearance, and I have seen the whole area, continuous substance as well as inclusions, *excreted* by a wave of contraction in the endosarc. Outside, it seemed to be a flocculent mass, which soon disintegrated in the water and was dissipated. Later, after a considerable interval, another contractile vacuole was formed in the endosarc at another point, and the surrounding protoplasm of that region soon gained the more fluid appearance which usually characterizes the region of a contractile vacuole in the forms which gave these facts.

It is no uncommon thing in *Amœba proteus* and in other Protoplasta, notably the Heliozoa, to cast out thus portions of

their living substance, which seem to have become in some way weakened or effete.

[30] The so-called *membrane* of the contractile vacuole is after all but an unstable, areal organization of the interalveolar substance, as a contractile pellicle, or membrane, and besides its periodic effacements, is subject at all times to the same flux of its substance as is the surrounding network. Yet in so far as it is at times so modified in its structure and reactions as to form, though but fleetingly, an area of organized physiological reaction; and to function at such times as a contractile membrane; it is a true organ of the cell.

It is a substance organ in the same sense as are all contractile pellicles.

To relate in detail all the phenomena observed in the contractile vacuole of *Amœba proteus* alone, the rhythmical substance and structure changes, would fill a large essay, which it is hoped to edit separately at some future date.

In some Protoplasta, the number of contractile vacuoles is not fixed, new ones arising capriciously in their midst. This is true of some Ciliata also.

I find that the contractile vacuole of Protoplasta is, as a rule, but not always, discharged to the exterior of the mass. At times, collapse takes place before the periphery is reached.

A strange intermittent contraction is found in the pellicle which lines the pharyngeal and œsophageal cleft in the Vorticellidæ. By an annular constriction, the lower end of this cleft which runs from the peristome down to the lower end of the body is cut off, and then with its contents forms a sharp-ended, pear-shaped sac full of water and of ingested food. The contraction by which it was cut off passes on behind this sac, pushing it further and further from the end of the now much-shortened tube. By continuance of this same contraction in a wave-like impulse, the sac is forced upwards through the endosarc, along a gracefully curved course, until by pause of the contraction it rests at some point. During this time, by relaxation of the pellicular substance, it has yielded still more

fluidly to the laws of its structure, the foam structure, and becomes a spherical food sac.[1]

Here we have a physical pellicle of the substance, formed at moment of a splitting apart of the endosarc, modified into a true contractile pellicle. After functioning for a time in this way, it is as a viscid fluid transferred to another portion of the endosarc, and there being for a time relaxed, functions merely passively and permits the passage of fluid through it. Then it may more or less often function again as a contractile membrane during the digestive process. Finally, it is again forced outwards by a contraction wave of the surrounding substance and beneath the peristome collapses, expelling its contents to the exterior, after the manner of a contractile vacuole ; *or it may itself also be expelled by the endosarc and perish as waste matter with its contents.*

Beside the formation of digestive sacs, these activities of the substance were seen to be made use of to rid the organism of unwelcome presence in the pharyngeal cleft of large numbers of bacteria which were whirled into it by the cilia. Under similar circumstances many rotifers would simply turn their digestive tract inside out, and so get rid of the intruders.

Here, with no visible nervous organization, the same result was had in rather a more complicated way; for the end of the pharynx, after being pinched off, was forced all the way up through the body mass and expelled, walls and contents at once into the water.

[31] In a single life phenomenon there is here shown a selective power of the substance; a migratory power as a substance organ ; metamorphosis of both substance structure and substance function; rhythmic changes of viscosity; and above all there is shown a correlation of impulse, a coördination of these activities throughout the entire mass, which is as perfect as that seen in organizations, where, to make it more comprehensible (?), there are enormously complex systems of structural modifications of the substance.

[1] These appearances were construed by Ehrenberg into a complex œsophageal structure.

To sum up all that has here been brought forward as to pellicles.

[32] Pellicles are of the interalveolar substance; and we shall presently see, that here, as elsewhere, the substance preserves *in toto* its inherent powers; so that there are not found in masses activities and characters, which are not found also in pellicles and small areas of the interalveolar stuff — areas so small that we cannot assign a limit to their minuteness.[1]

Pellicles are, characterized by a hyaline, and, with all but the highest powers, a structureless appearance. Their inclusions are for the most part fluid; if we exclude the so-called "granules," they are optically wholly so.

(a) Pellicles, whether as passive masses of interalveolar foam, or as contractile membranes, are organizations of the two groups of elements of protoplasm, on a basis of its visco-fluid foam character.

(b) This organization is in direct correlation with physiological activities of the substance; and hence I hold pellicles to be true substance organs.

(c) They represent the necessary primitive type of physiological organization of the substance; and are therefore typical of the primitive type of substance organ.

(d) They epitomize also all typical substance organization for reaction, in character, to environment.

(e) They are the primitive, as they are still the characteristic, end-organ of the living substance, as such.

(f) They have, therefore, in this respect also, the character of all true ectosarcal formation.

(g) Pellicles are the primitive ectosarcal formation, and are, in their origin as well as function, typical of all ectosarcal formation.

(h) Because of both their form and function it seems to me impossible to deny to pellicles the value of membranes, of living membranes. For the substance as such, they are membranes *par excellence*.

There is the more reason for this view since all those struc-

[1] See Activities, — also Substance as Such.

tures to which is conceded the value of a membrane arise as a simple or complex pellicular membrane.[1]

[33] In the pellicles of artificial froths, osmosis is controlled by the passive physical conditions. In living foams, osmosis is controlled also by changes in the pellicular substance, which are correlated with a physiological function or power of the substance (contraction). This is proven by the fact that existing physical conditions are in a moment set aside under such diverse stimuli as are supplied by reagents, or even mere pressure or shaking; the visible phenomena in all cases coinciding with those correlated with contractile function of the substance in typically contractile areas.

ALVEOLAR LAYERS.

[34] Although in living protoplasm a true "alveolar layer" of Bütschli may very often be found beneath the pellicles which limit masses, and also those which surround inclusions, as the contractile vacuole, these appearances are in most cases transitory or transitional only, and are constantly disturbed by the action of other forces. Excepting cuticular and other substance structures which have organized contractile activity, — and these may occur at any point in a mass, — so-called "alveolar layers" among the Protozoa and among many Metazoan structures are subject to constant disturbance.

(a) On the other hand, in dead or dying protoplasm, in some peculiarly relaxed, inert, or partially atrophied areas and masses, in short, wherever and whenever there exists a marked relaxation of the substance, alveolar layers are beautifully distinct, and form at points in relation to the mass which also bear out their physical origin.

It is significant that in almost all preserved material, especially where the method has been rather slow and sufficiently

[1] *Membrane* (Century Dictionary definition): A thin, pliable, expansive structure of the body; an expansion of soft tissue, or part, in the form of a sheet or layer, investing or lining some other structure, or connecting two or more structures. The term is used in the widest sense with little or no reference to the kind of tissue which may be involved, the membranous quality depending upon thinness and pliability, not on texture or fabric.

delicate to avoid gross vacuolation of the structure of Bütschli, alveolar layers are marked.

The fact that in the living substance these layers are less stably present than Bütschli supposed does not militate against his theory of the structure of protoplasm. It is, on the contrary, enforced, because the moment the substance as such is released from certain physiological controls, it proves its physical form by acting as a mere visco-fluid foam.

[35] While I find alveolar layers to be expressive of the physical form of the protoplasmic foam, they are not necessarily due to this alone, but may express also effects of physiological states and physiological activities.

Many alveolar layers given by preservation methods express an osmotic vacuolation of the living structure. This can be proven by use of reagents on living material under the microscope.

[36] Contrary to all the conditions found necessary by Bütschli for alveolar layers in artificial foams, I find the living substance forming freely, in a moment, at any point in its mass, and while the general structure of Bütschli is of markedly irregular size, and the mass or area is of marked viscosity; perfect alveolar layers.

The most interesting instance I know of this is afforded by the formation in developing echinus eggs of a perfect and *double* alveolar layer internally to the cell-mass. This afterwards becomes for a short time part of the external peripheral layer of the new cells, the split taking place between the two rows of vesicles.

[37] Marked viscidity of a mass, or area, of protoplasm seems no bar to formation of a very perfect alveolar layer; the irregularity of its existing structure, no impediment; nor, on the other hand, is the fluidity of a living area or mass any guarantee that there we shall find a definite alveolar layer, except more or less unstably. The living foam, then, is able in this respect to defy, or set aside, those controls which rule the purely artificial foams of Bütschli.

In artificial foams the finer vesicles tend to range themselves peripherally to the mass, the outermost layer, in foams which are not very viscid, being the alveolar layer.

[38] I find in living protoplasm that the size of the vesicles of Bütschli's structure cannot be brought under any rule correlative with their position in masses.

In any portion they may be large or small, or they may be either in turn, and their organized arrangement extend in any direction.

Except the fact that the pellicular formations are always of the finer foam of the interalveolar stuff, it is impossible to group in point of size the remarkably diverse structural facts of protoplasm.

The same results are attained by the same creature, within short intervals of time, by widely different distributions of the substance elements. Peripheral areas may be coarsely or finely vesiculate. They may be very viscous and have a finely subdivided structure, and then one may group together numberless instances of similar coincidence. They may be very viscous and have a very coarse alveolar structure; and here again one may summon many like cases. They may be markedly fluid and have either coarse or fine structure. A coarsely structured area may at one moment be very fluid and at another very viscid. The same is true of an area or mass having marked viscosity. In such forms as *Amœba radiosa* the substance may be watched for days varying from moment to moment its play amongst such phenomena.

These changes of physical state are most instructive, for they represent the characteristic powers and activities of the living substance.

AREAL DIFFERENTIATION.

For substance differentiations, as found in general researches among many, more or less scattered, organisms, it is difficult to lay down general rules. It might seem well-nigh impossible, so contradictory are the evidences when followed along some lines. Yet it is hard to work long on the substance as such without becoming sure that there are generalizations to be made, and hardly to be escaped, since along other lines the habit of the substance is clearly defined.

[39] Thus much is certain, that wherever was found organized

physiological activity, there was found also physical organization of the two groups of elements of Bütschli's, or a finer, or a coarser, foam structure, with or without further physical modification of the given interalveolar structure. As to the observer's perception, this organization arises sometimes simultaneously with the activity, sometimes precedes it, and may outlast it, but always accompanies it.

(a) It does not necessarily follow that the structure visible to the observer in a physiological area is that which is to be correlated with the given function; nevertheless it is true, as will be shown, that function and vesicular structure are indeed too closely linked for us now to set them apart.

(b) Capricious as seems the substance, unstable and incalculable as are its manifestations, there can yet be found certain broad laws, or rather habits, of structural arrangement under which it is wont to express itself.

(c) Under the head of pellicles somewhat was indicated of the manner in which masses of protoplasm are subdivided and differentiated structurally by arrangement of the continuous substance and the inclusions, and by the character of these two sets of elements. And to pellicular formation much of the optical, as well as physical and physiological, differentiation of areas is due. (See also Ectosarc.)

The majority of facts relating to these things are so inextricably correlated with phenomena of the substance as such, which must be grouped under the head of activities, that they will be treated of in that section, but some few important generalizations are offered here.

[40] Two groups of areal differentiation are most marked, —those in which the function is of a vegetative sort, and those in which it is organized or emphasized irritable or contractile function, or both.

In the former case the continuous substance has not usually that marked refractive and viscous emphasis, stable or rhythmic, which peculiarly characterizes the other group of structures, yet such there may be, at intervals during active secretion, as was seen in the gland of a certain rotifer (*Megalotrocha*), which, situated by the point of exit, pours out a glairy sub-

stance about the eggs as they leave the body.[1] There are cases in which the two sorts of structure are combined. In these the substance, both as such and as area or organ, functions for "secretion."

In areas having marked glandular function for the organism, the inclusions corresponding to Bütschli's structure are apt to be much enlarged. It is noteworthy that certain brain and ganglionic areas of some rotifers showed such a state of things.

Areas whose function is not for displacement but in gross chiefly of a chemical nature, are thus of the vegetative class. Hence all areas where the substance as such occupies itself chiefly in digestion or assimilation processes join this tentative group.

[41] Wherever areal function is markedly irritable or contractile, the inclusions of the organized substance are uniformly fluid, and the discontinuous element is evenly distributed with respect to the course of organized action of the continuous element.[2] It is evident that the elastic, contractile, continuous substance *has freest physical opportunity when its inclusions are fluid and uniform in size.*

(a) Further, whenever in areas characterized by heterogeneity of inclusions there arise organized activities of this sort, however fleeting, a precisely similar state of things is associated with them. In development of many eggs the direct action of the substance with respect to its different inclusions is striking. Solid substances, such as yolk or pigment, are segregated or deported temporarily from areas in which activities of the sort under discussion are to appear. Sometimes these areas are in relation to individual cells, sometimes in relation to the whole coming organism as a substance mass.

[42] Wherever, in short, the substance is preparing itself for organized contractility or irritability (if, indeed, we may so far separate the two), it provides for itself just those physical conditions which offer greatest vantage.[3]

[1] In this form I find there is a special opening for the egg to pass through, quite distinct from the cloacal opening, and situated just above it.

[2] See Striation; also below, nervous areas.

[3] Obviously this might be conversely stated, yet, it seems to me, with less justification as yet.

[43] The most readily noted feature of such organization is uniformity in kind, size, and arrangement of inclusions. But this is in most cases secondary in importance to differences in quality, structure, and position of the continuous substance. These things are as true of contractile and transmissive areas in the Metazoa as in the Protozoa; and portions of one or many "cells," may be involved in these modifications.

(a) In areas formed for interaction with environment, whether limited to pellicles or involving an underlying alveolation, fluid inclusions are gathered together, arranged with great uniformity, and often subdivided to a point of great minuteness, which latter change involves, of course, a physical extension of the lamellar substance. (For the full significance of these things the reader must see the later sections.)

(b) Such are ectosarcal formations, and such the arrangement of the elements wherever the substance meets internal contacts with organized reactions characteristic of ectosarc.

(c) All areas to be grouped with ectosarc, that is, all areas which are formed of interalveolar material, with or without fluid inclusions of the structure of Bütschli, have the same character.

[44] There is a marked habit of the substance to meet all contacts involving a number of the alveoli of a given structure, with organization of its elements in such a way as to produce an ectosarc-like formation. This may be formed of inter-alveolar material alone as a pellicular modifier, or may involve more or less of the structure of Bütschli.

(a) In the formation of ectosarc there is a tendency to reduce the structure by subdividing the alveolar inclusions.

(b) There is a tendency, too, in such areas, whether so subdivided structurally or not, to increase of viscosity.

[45] I find that true optical homogeneousness, or structurelessness of protoplasm, is most often produced by minuteness of structure, rather than by mere stretching of alveolar lamellæ. The latter state produces, of course, a less dense and refractive substance, while the former produces a more dense and refractive substance. So-called, as well as veritable, optically structureless protoplasm is commonly denser, more viscous, and

markedly more refractive than the structured areas. While I agree with Bütschli that we are often deceived, as in the instance he cites, and which I have also verified, into believing an area of protoplasm to be structureless because of a greater tenuity, by stretching, of its alveolar lamellæ; I have seen numberless times the origin from visibly structured areas, of true, optically structureless protoplasm, by progressive subdivision, or reduction, of the structure of Bütschli. This often takes place with marvellous rapidity, and to a point of minuteness causing great difference of optical quality, and the area so formed may be very fluid or markedly viscous.

It is in no other way that the ordinary structureless portions of ectosarc of Amœba, etc., are formed. True, there are very hyaline and delicately structured areas which arise without such reduction, except near the periphery, by outflow from the endosarc of interalveolar material, with or without fluid alveoli of Bütschli's structure, but it is reduction phenomena which give a veritable structurelessness of appearance. Both sets of phenomena may be witnessed within a few moments in an *Amœba radiosa* which delights in varying its activities a thousandfold. Even without any perceptible change of form in the animal, which may at the time be somewhat rigidly extended in the water in the form of a star, of four, six, or any moderate number of arm-like rays, or spread out as a fan-shaped film; the structureless substance will in a variable time be resolved again to a very marked structure of Bütschli.

At both times, under sufficiently low powers, the ectosarc will have an optical structurelessness, and possibly also a greater refraction than usual; yet in one case the structure of Bütschli as such has been obliterated, and in the other case is again present. The increase of refraction in the substance may be seen to be caused by a change in quality of the interalveolar material, so that the meshwork of Bütschli's structure stands out refractively, as thickened trabeculæ, under lower powers than are usually needed to resolve it. Structural reduction in the living substance does not always result in thinning the interalveolar material. Pellicular and interalveolar material furnish commonest instances of apparent optical structureless-

ness, yet in them a true structure has been found, and one undergoing such modifications as are found in the coarser structures. It is necessary to distinguish between visibility of areas and visibility of the *protoplasm proper, or continuous substance,* for the character of its inclusions may make a whole area distinct or prominent, while its protoplasm proper may at the same time be very fluid and not so readily seen as that of adjacent areas which *in toto* are less conspicuous ; but the optical phenomena in such cases are markedly different from those in which areal visibility is due to quality of the continuous substance.

[46] I would group all areas having the origin and character of the ectosarc of protoplasts under the head of ectosarcal formations or modifications of the substance. As stated above, all physiological pellicles fall naturally into this group.

To glance for a moment at the formation of ectosarc by Amœba may enable the reader better to understand the argument. The point involved is of radical importance. An *Amœba proteus* is at all times covered by a variably thick, hyaline layer, whose surface forms an unstable pellicular membrane. But when at times, in the heave and flow and evanescent shiftings of the protoplasm, there is at any point a rush of substance that wholly or partially pushes, or breaks through, this layer or is yielded to by it, so as to come in more or less close proximity to the water, the phenomena may be said to represent to some extent a primitive formation of ectosarc. This may have been primitively a purely physical incident, taken advantage of by, or necessarily causing physiological or physical vantage for, the living substance.[1]

One does not, however, see the whole mass covered at any one moment by such an area ; that has been the work of ages, and the present habit, while typifying a more primitive act, is of course a much modified and extended form of it, for in the simplest Amœba known, the plastic substance is already very old and full of registered experience.

Watching an initial formation, not a mere displacement, of ectosarc, one sees a gradual, or more or less sudden, or even a spurting, outflow of what has been called the hyaloplasm of the

[1] See New Structural Formula.

endosarc, that is, the more hyaline, fluid, colorless portion which does not carry solid bodies or nutritive material in an unassimilated state. This is already, in *esse* as well as in *posse*, an ectosarcal formation, and may be seen to function in a characteristic, organized way as it is mingled with the true endosarc. Besides that hyaloplasm which is formed of the structure of Bütschli, there is an interalveolar, hyaline substance, the finer foam, which also flows out with, or besides, this, and the two structures mingle fluidly amongst each other. In such ectosarcal outflow, there follows the first impulse a more or less active motion of these alveoli amongst each other. There are so many modifications in individual cases of the result in particular, that it is difficult to seem to describe accurately any one instance, unless to those who hear all are familiar.

The damming back of outflowing substance by a rapidly effected pellicular formation of ectosarcal character, or by obstruction of already existing pellicle or ectosarc ; as conflicting with the onward rush of material from the endosarc, causes often in the newly formed ectosarc a kind of boiling motion which comes to an end variably soon according to circumstances. Where the barrier is an existing ectosarcal formation which does not readily yield to the outflowing substance, the direct course of this is changed to more or less lateral flow. The alveoli of Bütschli's structure then become less freely mingled with one another, as if the impelling force ceased to act, or as if there arose an increased viscosity crossing the path of the latter, or sometimes following it in point of time and impeding the fluid motion. Such viscosity is understood from certain optical changes in the quality and action of the substance, or by changes in structure. There is little doubt that further progress is often checked by formation also of a more finely structured, and therefore more viscid and resistant, area in the advancing substance itself, along the line of its contact with the existing ectosarc ; just as in this latter when it came in contact with the water, a similar area was formed, checking in the same way the substance following fast behind.

If the outflow of hyaloplasm has burst through an existing pellicular membrane into the water, or runs very close to this,

there is more apt to occur this phenomenon which is very characteristic of ectosarcal formation, and which has almost unbounded possibilities in an evolution of protoplasmic structures, as will be shown further on,[1] and in still another publication now in preparation for press. I speak of what I shall call *structural reduction*, that is, a redistribution of the elements in an existing structure so as to group them into a new and finer foam structure. The vesicles of the existing structure become quickly more minute, and should subdivision continue, yet finer and finer, being always increasingly small towards that outer side or portion of the area which is peripheral as to the mass. Structural reduction takes place in a number of ways. The alveoli of Bütschli's structure were seen at times to be cut in two by constriction, or pinching off, just as a contractile vacuole, or as the œsophageal cleft of Vorticellidæ divides. Sometimes the interalveolar substance spins itself into and across fluid inclusions; sometimes there seems to be local relaxation of interalveolar or continuous substance, causing redistribution of alveolar inclusions.

But however it may be done, the fact is certain that it is done, and that in most cases of ectosarcal formation there is more or less structural reduction and reorganization of the two groups of elements, which may or may not extend itself to the interalveolar structure where it is visible by change of the optical quality of this substance[2] or again may be confined to this alone.

The amount of such reduction varies with the circumstances of formation, or even, to all seeming, irrelevantly to these. Where large areas of new ectosarc are brought into direct peripheral contact with the water, or general environment of the mass, there is more structural reduction than where the outflow is checked by presence of existing ectosarc in a thick layer. It was the optical appearance of these phenomena as seen with powers too low to resolve structure, which gave earlier observers an idea that the substance became coagulated on contact with the water. As a matter of fact, ectosarc may be

[1] See Selection of Environment.

[2] See Striation.

far more fluid than endosarcal areas, although it usually is seen in a more viscous state.

One interesting unstable area of structural reduction which I think has not yet been described, was seen as a variably present and fluctuating area surrounding the nucleus in Amœbæ. Very finely vesiculate, often passing into true optical structurelessness, when it had an effect of brownish or yellowish hue and was of a dense and peculiar appearance, this viscid mass adhered to the nucleus and was carried along with it, as the endosarc rolled hither and thither. Less transparent and also far less refractive, though quite as dense nearest the nucleus, it reminded one much of the "achromatic" areas in embryonic masses.

Its amount was greatly varied from minute to minute, sometimes being at least one-sixth the width of the cytoplasmic area, at others merely a sticky-looking stratum close to the nucleus, as if the cytoplasmic pellicle were unevenly augmented. Whatever its thickness, it swept along with the nucleus, holding its place as an almost solidly attached substance while its outer portions were drawn out as threads and viscid-looking processes in the cytoplasmic flow over its surface, so that it looked somewhat like a caged Heliozoan in closest physical union with the surrounding fluid alveolation. No special life phenomenon was seen to be correlated with the presence of this area.

It is not only at time of initial formation of ectosarc that the phenomenon of structural reduction is seen. In ectosarc long formed and quite stably persistent through long periods, and in ectosarcal organs and areas, similar redistribution of the elements takes place at times, changing the physical form of the substance locally or throughout the whole area from a perhaps marked and uniform structure of Bütschli, or finer forms, to others progressively finer until a point of actual optical structurelessness is reached. From this state redistributions may later bring before us again a true structure of Bütschli, not the former one but another, in which it is more than likely not one particle of the elements holds its initial relative position as to the others or as to the whole mass.

It is important to remember that in the living substance true ectosarcal layers are formed at any depth and in any relative position and of any form, as readily as they arise externally to masses; and that such formation may be the work of a moment only.

[47] Ectosarcal formations often arise by outflow of the interalveolar substance alone without implicating or even visibly disturbing an existing structure of Bütschli.[1]

[48] All ectosarcal formations appear to be essentially organizations of the continuous element involving redistributions of the alveolar inclusions; and to be formed for physiological function; for organized reaction of the substance as such in its own character to environment.

[49] In many areas so formed it seems to be of no moment which portion of the continuous element is in contact with any visible vesicle, but all portions can react alike near all portions of the general inclusion fluid. In other words, there is in such areas a homogeneousness of the continuous element and equal homogeneousness in general character of its specific stimuli. Any part of such areas is, therefore, for the time being physiologically equal to any other part in these respects.

(a) Yet any part of the area may show specific differences of action, which are secondarily referable to either local differences in its own finer structure, or inclusions, or slight differences in kind of the inclusions of the given structure. Such local specific activities are always directly referable to characteristic changes of the continuous element.

[50] Although true protoplastic ectosarc, as it is best known, is commonly seen as arising in response to contact with external environment, it may hardly be thought that such areas are in general a result of such contact, for in the majority of cases they are formed before, often long before, the occasion of their use. Sometimes they may never even reach that environment for reaction to which they have been moulded. In the formation internally to a Protozoan's mass of pellicles and pellicular organs which, till after completion, are shut out from their

[1] See Activities.

specific contact as organs with external environment, are seen instances of areal differentiation on an ectosarcal basis preceding physiological function: of vesicular preformation of substance organs before the actual opportunity for their use has arisen.

Among the Metazoa such redistributions are common and numerous in development of cells and organs.

Within the endosarc of Amœbæ and other Protozoans one can see, fleetingly formed from moment to moment, small local areas of true ectosarcal character; that is, showing a uniform distribution of the two sets of elements in relation to each other, with homogeneousness of both in general character; and with certain organized, though fleeting, activities which are characteristic of true ectosarc. Besides these, there are the stable pellicular formations about nucleus and food sacs and the contractile vesicle, which are all organized areas of interalveolar stuff involving more or less of the structure of Bütschli. Like other contact areas, or substance organs, they are all characterized by fluidity and uniformity of their inclusions.

Such true and stable alveolar areas as are found in Protozoa are, as a rule, marked by organized contractility, so that these also are less expressive of physical form than of the correlation with the foam structure of certain intrinsic powers of the substance.

With few exceptions, ectosarcal formations show with variable intermission contractile activities. Even the nuclear pellicle cannot be excepted, for few nuclei do not from time to time have amœboid changes of contour more or less marked. Wherever in a Protozoan or Metazoan contractile activities were visible as such, there was an organization of the elements and structure typically ectosarcal, no matter how fleeting the physiological manifestation might be. The structure might be stable, or might not outlive the activity, but in all cases organization of the continuous substance upon a fluid-inclusion basis existed at the moment of function in the functioning substance, and was exactly of the sort seen in typical ectosarcal areas. Wherever preparation of areas for organized contractile function was watched, the process was seen to be not other than that typical of the formation of ectosarc.

Whenever organized contractility appeared for the first time in any existing, or new, irregular ectosarc, it was preceded by thorough and systematic reorganization of the elements on the same basis as that of the initial formation; the interalveolar substance having always the leading rôle.

And wherever such a characteristic arrangement of the elements already existed, organized contractile activities were seen to arise at some moment without further change in the existing structure than such as pertained to that rhythmic qualification itself.

[51] To sum up: contraction was found always associated with an organization of the elements which is typically ectosarcal; and typically ectosarcal areas were found to be characteristically contractile. Organized contractility was not found except where the elements either of Bütschli's or of the interalveolar structure were directly or indirectly shown to have such a constitution.

It may seem, perhaps, that the same things have been said a great many times over in slightly different ways. This is exactly what nature does with these facts; and it is only by following constantly along different, yet closely kindred, lines up to the same conclusion that one gets a realization of the truth in this matter; a fundamental truth it is with respect to the living substance and its habits of self-expression, and there is none other, I believe, so important in evolution.

[52] In the light of such facts, ectosarc appears to be the type, or illustration, of all characteristic substance organization; for, as it will be shown that contractility is still the basic, typical activity of the living substance, as far as this can be seen to act, so also down to this limit is ectosarc formation a fixed, physical basis for this activity; the basic mode therefore of organization of the characteristic powers of the living substance. That this relation is indeed inevitable from the nature and relations of the powers and the form of the material, will be shown in the section on contractility and in that on the new formula offered for the living substance.

It has been stated that the stability of a structure of Bütschli is no guarantee of stability of the living substance as such in

that area. This is true whether the area is one stably organized for contractile activities or vegetative in its habit.[1] Even in strongly contracted masses and areas having a marked structure of Bütschli there are numberless local disturbances of the interalveolar substance, even transposition of this which is yet responsible for the structure and functional activity of the area in gross. After organized function throughout the area, portions of the contracted substance relax, but the characteristic organization of the structure remains marked and stable in the whole area. This shows certainly that not all of the continuous substance is necessarily involved in maintaining contraction of any area, on the basis of a given structure.

In the few Metazoan organisms whose development I have watched, there is a more or less gradual formation, peripheral to the mass, of an area which can be grouped with typical ectosarc alone. And for each so called cell mass, or nucleated and pellicularly separated subdivision of the general mass, there is also such a layer.[2] As the Metazoan substance, in its life-rhythm as organism, approaches an adult stage, there gradually comes to be by successive reorganizations of its elements, an area of true ectosarcal type in gross. This has been called the ectoderm, and is formed of "cells," to the general substance of each of which the same typical structure may be extended in a variety of ways. Of such Metazoan ectosarc are made, as a rule, all areas of the mass, or organism, which as organs correspond in function with true ectosarc in Protozoa; that is, which act as *intermediators* between the mass and its external environment. True ectosarcal formations of the Metazoan are, however, by no means confined to such cells; but most, or perhaps it may even be said, all other cells form to some extent such areas of their substance.[3] Nor can these be held identical in any way with that purely physical ectosarc of artificial foams, since in their origin the living substance seems to be neither dominated wholly, nor inhibited, by those physical conditions which Bütschli has shown us do, in artificial foams, produce, or forbid production of, such areas.

[1] See Activities — filose ; also Contractility.

[2] See Activities, starfish and sea-urchin development.

[3] See Striation.

[53] Ectoderm with its products is but either repetition in gross, or a multiplication by repetition, of causes and effects which form the Protozoan ectosarc and its products. Beneath the seeming demarcation of "germ layers" with their products, the substance expresses itself again, more definitely, in a series of minute but kindred structural organizations of the elements. These are to the substance as such what the germ layers are to the substance as organism. There are throughout the whole Metazoan organism countless areas of wide range in size; some restricted to the limit of single cells, others passing through large numbers of these, some of most minute vesicular structure, some having a beautifully marked structure of Bütschli, or even coarser vesiculation; but all taking their rise from the general or "undifferentiated" protoplasm; all functioning in a kindred way towards substance environment; and all true ectosarcal formations in origin, structure, and activities. The same is true of endosarcal areas, for these are found in strictly ectodermal regions and cells of the organism.

Physical nature heals the wounds of the living substance with a frail pellicle of continuous substance; physiological nature supplements, or supplants, this as rapidly as may be with a formation of ectosarc. In simpler and more primitive types of organism this service is performed by interalveolar substance, often aided secondarily by areas of Bütschli's structure. In more stably and complexly organized, cellular types the same surgical office is given by protoplastic activities of neighboring cells; by wandering cells, as leucocytes, or migrating cells, and as far as possible the damage is thus primarily repaired.

By so much of experiment as was made, it is certain that living protoplasm tends to protect itself, directly or indirectly, by various devices from unsympathetic environment, albeit of a kind never before experienced; and to protect its internal environment from change thereby. Such devices are of a nature which seals the substance for a time from intrusion of adverse or disturbing conditions, and bar it in with its own existing and intrinsic conditions acquired under more favorable auspices. That is, the living substance shuts itself up with its

own internal resources, its hoarded specific environment, so that for a variable time it becomes wholly independent of external environment, of even the element it usually respires.

From the formation of ectosarcal areas as external protection, to the natural habit of encysting, so common among the Protozoa and retained by protoplasm even among such highly differentiated forms as rotifers, to the self-sealing habit of snails, etc., and beyond these to the habits of hibernating found among the higher animals, even mammalia; the phenomena are strictly to be grouped together under this interpretation.[1]

Through a wide range of forms, protoplasm makes use of ectosarcal layers for purposes of temporary isolation to a more or less complete degree from the direct influence of external environment. The purpose subserved may be an economy of energy, and of material both as hoarded reserve and as a factor of immediate environment during metamorphic changes; or it may be purely protective during adverse conditions of environment. A very common thing is for part of the organism, or all of it with small local exemptions, to be superficially protected from external environment by such formations more or less modified secondarily; and such is the origin of all exoskeletons, and indeed of many endo-skeletons also.

The lower forms, and also the higher forms in embryonic stages, make large use of ectosarcal layers produced from their mass so as to form distinct membranes which either produce substance for a non-living membrane or themselves atrophy later and are discarded after the need for seclusion is ended. The striated membrane in Echinus eggs is of this sort. I have watched the progressive formation of silicious capsules in a fresh-water Radiolarian, *Clathrulina elegans*, upon a basis of a coarsely vacuolate peripheral layer of ectosarc, and noted an ectosarcal origin for the stalk; I have watched also the gradual formation, by progressive rearrangement of the elements with subsequent chitinous transformation, of the very complex capsule of the winter egg of the fresh-water Polyzoan, *Cristatella*.

These phenomena are one with the partial independence

[1] See Selection of Environment; also Fosterhood.

and physiological isolation gained for different areas or substance organs by pellicular formations of ectosarc. When looked at from the standpoint of protoplasmic habit, they must be regarded as continuous with the protection by ever increasingly complex and complete ectosarcal areas of all portions of the organism not concerned in the ingestion of food; and finally, with the systems of protective apparatus which, as tactile, and as offensive and defensive structures, guard at last even those weaker regions. The original formation may undergo more or less subsequent modification by secretion, or deposit, within or about it, of non-living material, such as chitin, silica, or the like. The actual living substance may be withdrawn, or may be gradually atrophied. In many cases it is impossible to say whether it is still present at a given stage, or whether it has been withdrawn or atrophied.

The function of secretion does not inhibit in the substance, nor imply its renunciation of, typical contractile characters; on the contrary, the latter may accompany the former to a marked degree. There is even strong reason for supposing that the function of contractility is always correlated with more or less excretion from the functioning substance, and here again it must be urged that it is most difficult for us to draw a line as yet between substance secretions and substance excretions. For we are dealing always, it must be remembered, with a complex series of alveolar structures, not with one alone, as Bütschli's, for instance. Rhythmic, or irritably responsive, contraction most frequently accompanies a secretive function, and typical ectosarcal characters are very favorable to this state of things. By contraction, interalveolar vesicles may readily be emptied into the larger inclusions of Bütschli, and from these, which are storehouses of secretions as we know them, contractions of their interalveolar material pour the fluids. In strict sense, though not in common usage, the substance produced by areas and organs should be called *excretions* when exuded from those places of formation, and secretions so long as they are considered *in situ*, although here they may be again strictly excretions of the living substance, that is, of the continuous substance.

Substance differentiation as seen in Protoplasts was illustrated above by a specific description, for which *Amœba proteus* was used. For differentiation of the living structure as found in Metazoan organisms, a starfish egg watched through its development is, perhaps, as beautiful a typical illustration as the student can have. As it lies in the water before maturation with its nuclear sac still perfect, it presents to the eye a mass of living substance having already area within area of pellicular and alveolar organization. Thereafter the history of development is truly a record, from moment to moment, of more or less unstable permutations, transmutations, and metamorphoses of such structural differences, having complex, rhythmical relations to the substance as such, to the substance as organism, and to the life history of the race substance.

At such a time as I have chosen, there is seen within the outer protoplasmic pellicle of the egg the mass of general cytoplasmic substance, where changeful rearrangements of the foam vesicles arise and pass like dissolving views. The vesicles of Bütschli's structure have seldom a spherical, but rather an irregular contour. They are drawn out of shape still more from moment to moment by local tensions in the interalveolar foam.

Within the general cytoplasmic area comes the nuclear area surrounded by its own pellicle which, in those cases examined, was formed of very small vesicles bounded on either side by pellicles of continuous substance. It was most like those intra-cellular formations which later form the new cell walls. The surface of this nuclear membrane yielded at times under favorable optical conditions finer vesicular contours which produced the "shagreen" effect.

At this stage, the general nuclear area is a much less dense, and optically much more fluid-seeming, area than the cytoplasm. That it is actually so was proven by pressing the nuclear contents out into the water through a mechanical rupture of this membrane and the egg membrane. Yet this nuclear area contains local modifications of its vesiculation, which have pronounced viscosity over that of the cytoplasmic area even. These are variably numerous, smaller, spherical areas, which

seem to repeat in minute the characters of the whole area, for they are surrounded by a pellicle of similar formation to the nuclear pellicle, and they contain yet other areas of the same kind as themselves, and these even others, so that the whole nuclear area is a very complexly differentiated foam.

Within the small spheres appear peculiar optical and physical modifications of the interalveolar substance, in the form of minute very highly refractive and dense masses. This is the "chromatin" substance. It is seen in greatest quantity in one, two, or even three of the largest spherical areas, but is sometimes found also in very small quantities in several others, or in one only, according to stage of maturation.

Two or more of the largest spheres, which contain the most of this substance, approach and coalesce with each other, until there is formed one sphere far larger than any of the others, and now optically very distinct also, because of the amount of the refractive chromatin it carries.

Some of the smaller areas break up and disappear from time to time, and so the whole nuclear area undergoes a thorough and continuous series of redistributions of its elements, many of these changes being carried on simultaneously.

The largest sphere becomes the egg nucleus which afterwards receives the sperm. Within it also, until the nuclear membrane is dissipated, goes on a ceaseless *shuffling* of the elements; the smaller spherical areas being thus changed into a more uniform arrangement which is bounded by the single pellicular membrane, and the chromatin substance being disposed in a seemingly continuous line of interalveolar material which forms the nuclear optical network. I believe that the rearrangements of the nuclear elements are continuous, and that there is never what may be termed a truly resting or quiescent stage. The phenomena become at times simply less obvious, that is all.

Even after dissipation of the nuclear membrane, and after perfecting of the new nucleus, so far as one can trace the facts, there remain small portions of the chromatin scattered about, or massed together, in the nuclear substance, and later in the cytoplasm. The presence of these was first noticed at Wood's

Holl in 1893, and afforded an explanation to me of the results then being attained by other investigators in fertilization of eggs from which the new nucleus had apparently been shaken entire, and also of supposed non-nucleated fragments of eggs. What the final fate of these chromatin fragments was I did not determine, being then at work along other lines. They might later have been carried to and even into the nucleus, or they may have had some special mission of their own in the coming development.[1]

It is not possible to describe, for it is not possible to grasp mentally, in even their grosser relations, all the changes which take place during the developmental phenomena so roughly indicated above; for the changes are so continuous, in their subtle modulations, and yet so kaleidoscopic in their effect on the mind which fails to follow, that directed, or even passive, attention is beaten at the outset. And then attempt at description is futile, for how can this, with its inescapable limitations, be applied to activities which are freely simultaneous in three dimensions of space? To try to grasp all, or even most, of those in a limited area is to be utterly baffled. Many years of observation could well be given to the changes which come about in formation or maturation of the nuclear area alone.

Dissipation of the nuclear pellicle is preceded by contractile waves in it, and later the component vesicles, loosing their hold upon each other, are carried away and mingled amongst the surrounding fluid substance; for the cytoplasm becomes for a time very fluid, from having mingled with it the watery contents of the nuclear sac. Later, this local fluidity is much decreased, and there is a general gain in viscosity of the whole internal portion of the cytoplasm, with marked increase in this respect towards the periphery of the egg.[2]

[54] Following up along the same lines the phenomena of fertilization and of cell-division, these were seen to be but more obvious stages in a long and never-ceasing series of redistributions and reorganizations of the foam elements of the living

[1] See Activities — filose.

[2] See above rhythms of viscosity in starfish and sea-urchin eggs.

substance of the egg. And it became evident that in the long and intricate series of these phenomena, one must learn to attach to each area in which is seen true organization, however fleeting, of the elements, the value of a true physiological area of the mass; and to rank it as a true substance organ.[1]

The very transparent nature of the larval stages of starfish affords large opportunity for study of the origin and primitive nature of many later substance organs. In such transparent forms as the Rotatoria one has an almost limitless source of knowledge on these points. Other creatures yield still more. From what is found in these, comes illumination for structures and processes less easily traced in less accessible protoplasm, which should enable us better to interpret results in preserved material.

[55] In all nervous or transmissive areas examined, was found an organization strongly akin to that of contractile areas, only still more emphasized in a peculiar way. The structural characters here belong peculiarly to the finer foam, whether the area involves a structure of Bütschli or not. Hence the true nervous or transmissive substance forms fibrils of continuous substance, which may be joined with, or woven into, any amount of combination by other modified or unmodified trabeculæ of the structure of Bütschli or of a coarser alveolar structure. Where these tissues are complex, the appearance given by most reagents is singularly false, producing an unnatural vacuolation which often simulates a beautiful, distinct structure of Bütschli.

[56] So far as I have seen in transparent aquatic creatures, the termination of all nervous or transmissive areas is in the continuous or interalveolar substance of a visible structure. This does not, as will be shown, preclude possibility of invisible filamentous extensions into alveolar inclusions, but all the direct and indirect evidence is for a special modification of the continuous substance simply ceasing at some given point in this.

The continuous substance is sometimes much swollen in

[1] See Activities — Cell-division, in this connection; also New Formula for the Living Substance, and Fosterhood.

single or isolated fibrils, tapering down towards its termination in the continuous substance to a less and less perceptible filament which clearly must end in the continuous element of the finer structure of the interalveolar foam. In other instances the fibril, or nerve line, of continuous substance is uniform in width throughout its entire length. The walls of the vesicles in most transmissive areas seem relatively very thick with regard to size of inclusions. In some ganglia examined the vesicles were, *per contra*, large with thin walls, and the whole area had a spongy appearance. Transmissive inclusions appear to be homogeneously fluid, like those of all true ectosarcal formation.

Between the sacs in which lie the nematocysts of Hydra, were seen delicate lines of alveoli which connected these in groups of variable number. The alveolar lines were in direct continuity, as to their continuous substance, with that of the alveolar pellicles forming the sacs. The optical aspect of the lines, which are to be resolved by the highest powers only, is exactly that of such areas as form the skin nerves and other fibrillar nerves in rotifers, etc. Watching a Hydra under stimulation, those groups of cysts between which I could trace this living connection, seemed to coördinate during discharge of nematocysts from that portion of the animal.

[57] In such transmissive areas I have seen no direct evidence of contraction, but that does not by any means negate the possibility of such.[1]

[58] Transmissive areas seem to be very stably organized in the cases where they appear as special protoplasmic structures.

[59] It must be noted here that all ectosarcal formations are highly transmissive in an organized manner ; differing in the matter and manner of transmission according to their specific structure. Wherever there is organized contraction there is also a certain sensitive transmissiveness which seems to be inseparable from such organization of the elements in homogeneous and specially continuous manner, and without breaks in the general state of the continuous element.

[60] In all ectosarcal formations which show marked struc-

[1] See Contractility.

tural reduction of the peripheral portion, there appears to be increased irritability to stimuli of all sorts, the *tactile* powers of the substance in the widest meaning of the term receiving emphasis.[1]

[61] The optical quality and structure of nerve lines of the continuous substance is extremely like that of the "granules," and like "chromatin" in all its different groupings as inclusions of the finer foam. The similarity of staining reactions of both these structures and also of nerve tissues is another likeness between them. In actual nerve lines of continuous substance I have not seen granules present as such. All these structures alike are more or less unstable organizations of the interalveolar foam, and can by redistributions along its lines become imperceptible as distinct areas, though they seem then to impart a characteristic optical quality to the whole area in which they lie hidden.

[62] To all of these there must be conceded the value of substance organs, as well as of organs of the organism; and the full significance of protoplasmic habits of self-expression.

As to those granules which, either in their specific form or in more finely diffused states, are inseparable comrades of the living substance, one is constrained to impute to them some direct relation to constant and characteristic activities of the substance in which they are imbedded, — that is, the continuous substance, for of this they are at all times inclusions, and at some times compound inclusions.

I could not determine whether the peculiar optical character of these inclusions were due to their included substance, or to the character of the continuous substance forming their walls and possibly a reticulum. I am inclined to think, however, that their refractive quality pertains to their form, and their marked tingibility pertains to the nature of their included substance. Later, when the facts have been given in relation to strial modifications of the continuous substance, this will be understood as not a mere guess, but as legitimate inference.

[63] Protoplasmic differentiations may be summed up as of

[1] This will be more fully discussed in a paper now in preparation for the press, dealing with end-organs, consciousness, etc.

two sorts, which are not necessarily separated in a given area.

(a) They are based on differences in character of the discontinuous substances or alveolar inclusions ; or on differences in character of the continuous element along optical and physical paths of the interalveolar substance.

(b) As to the first class, form, size, and arrangement, also physical differences in kind of inclusions, cause optical differentiation enabling one to separate areas from each other.

(c) Leaving out of count for the moment the finer foam structure, I find areal differentiation which is dependent upon the continuous element for its specific optical character, to be formed by a physical arrangement of this along lines dictated by existing, but variable, foam structure; with physical differences in its quantity and its appearance, the latter being caused by certain physical and physiological changes which have already been referred to and will be described more in detail in Striation and Contractility.

Physical variations of the foam structure, and the disposition of interalveolar stuff with its possibilities of difference in relation to any given foam structure; and these things in potential combination with the chemical variations ; surely offer a magnificent plasticity of conditions and causes for evolution to make use of. On this basis arise almost innumerable modifications of rhythmic, or intermittent, optical and physical emphasis and their associated changes, in form of alveoli, etc.

[64] With these possibilities even Bütschli's structure offers wide range for areal differentiation; but when, as frequently happens, this is carried down to the finer foam and its reductions,[1] the opportunities become so multiplied as to sate imagination.

Nor is it found in fact that the living substance has ignored the opportunities.

[65] In ectosarc is seen the type of substance organization for extension and correlation of physiological function. The connection between the two sets of facts is more readily understood when it is seen that in just this type of arrangement of the elements the active powers of the substance have full and perfect physical opportunity for their exercise and emphasis.

[1] See above ; also Contractility and Activities — filose.

The constant correlation of the two sets of facts was learned during careful study of contractile and transmissive phenomena.[1] It is in place here to glance at extension of physiological powers on the physical basis afforded by the foam-structure arrangement of protoplasmic elements, and peculiarly by an ectosarcal modification of this.

The myriad potential and achieved differences of physiological areas seem to be susceptible of at least partial analysis on this basis.

[66] In all areas whose office is direct displacement of the protoplasm — that is, whose function may be termed muscular — an increment of power, whether stable or unstable, seems to be brought about on a physical basis of a given structure. That is, more of the structure of Bütschli or of the finer foam may be involved, with the result at a given moment of a simple mathematical increase of the energy, which may be represented by $+$ or $\times$. It will be explained under Striation and Contractility that the contraction may be complex, and the first contraction on the structure of Bütschli may be continued by succeeding contraction based on the finer foam of the interalveolar material. In such case, of course, the same conditions extend themselves to the secondary contraction; but it is without structural reduction in the primary structure which may be coarser than usual.

[67] In all areas where the function is indirect displacement of the protoplasm, — that is, in transmissive and sensory areas, — I have found always so far a marked reduction of the foam structure of the interalveolar substance, proved, it is thought, by the optical evidences before advanced for such phenomena. Somewhat more is to be said on this head in the section on a new formula for the living substance, and much more in my forthcoming work on transmissive areas.

[68] The first sort of physiological extension may be termed *quantitative extension;* the second, *qualitative extension* of power.[2]

Below and behind such grosser differences in the foam struc-

[1] See Striation and Contractility; also New Formula.

[2] See also Selection of Environment.

ture of the living substance, lie partially, or wholly, concealed optically others whose limits we cannot know and whose nature is to be inferred to but a very small extent.

By themselves, chemical differences constitute a mode of areal differentiation of wide range within the limits of Bütschli's structure alone; and when the same holds true for the finer structure it is evident that what we can resolve of internal variations in organization of the living substance is, indeed, but a small part of all. That actual physical and physiological differentiation of the living substance far outruns our power to resolve local characters is certain. Hence optical differentiation is not to be taken as the limit, or sum, of organization, or of the physiological machinery of the living substance, but yet may be taken as typical of this.[1]

[69] In so-called "low" and "primitive" forms of life, the substance organization is seen to be very complex, if here as in the Metazoa the sum of all areal differentiations be taken as the unit of count; but it is less stable and more fleeting,— often, indeed, to the point of evanescence. Grosser structures are openly transmuted, whereas in the adult higher forms there is a more stable mask of structure behind which the substance carries on its unstable processes.

[70] Phylogeny is seen, from the standpoint of foam structure, to be a direct progression along these lines in this direction, and the types which follow each other in supposed evolutionary sequence seem to typify the results in gross of such progression.

[71] In all forms, from the lowest to the highest examined— subtly hidden often, it is true, beneath the stable as well as beneath the openly unstable structures — exist fleeting differentiations. Nowhere, unless secondarily modified so as to lose its vital state, is found a protoplasmic structure so stable and fixed as regards the substance as such that it does not permit these; nor does such stability of structure involve or imply renunciation of the instability of the substance as such.[2] Take, for instance, such very stably organized areas as the contractile cuticle of Epistylis, or the delicate skin of the rotifer, or muscle

[1] See next section, Activities.

[2] See pellicles and alveolar layers, above; and next section, on Activities.

bands of this, the crab, or even the tadpole or frog, and within the limits of the general stability of the whole area, or subdivisions of it, there may be seen to go on local transmutations of finer structure and even local modifications of the structure of Bütschli, as well as transpositions of the continuous substance. Scheme within scheme of simultaneous differentiations and physiological activities within a given area is thus opened up to us.

[72] In all it is the continuous substance and its organized relations to the alveolar inclusions which rank first; inclusion organization ranks second, yet may to large extent control the phenomena. The true interaction and relations of these two groups of elements are made clearer in later sections.[1]

[73] To sum up finally: in all the organisms examined, areal differentiations of the substance, in the threefold character of optical, physical, and physiological difference, express organization of the substance as such on a physical basis of the foam structure; and each area so formed, however fleetingly, must be understood as a true substance organ, within, or without, its possible larger relation of organ of the organism.

I have tried to iterate the above facts in such a way as to express somewhat schematically the aspect in which they present themselves to various points of view from which I approached the substance as such; and they play into each other in such a way as to make this seem a most fruitful plan of investigation for the student of living phenomena.

The few facts given here, like all those from which they were selected, are so inseparably correlated with the whole scheme of substance phenomena that they cannot be even fairly grasped until others, equally representative of other generalized substance phenomena, are at once within reach of the mind. Yet it is necessary in speaking of them to use to some extent the terms which all formulate, bespeaking the forbearance of the reader until the end of the argument be reached.

[1] See Contractility, and Selection of Environment by the Substance.

Protoplasmic Activities and Cell Division.

By the word "activities" I must be understood to mean such exhibitions of energy as directly or indirectly cause displacement of the living substance, — as such, as area, as organ, or as organism.

Useful as it seemed to learn somewhat more of visible protoplasmic structure, there proved to be other facts whose importance transcended this. There is no doubt that in protoplasm, as in artificial foams, there are structural differentiations which imply certain physical stress and controls, resulting from the mere physical conditions belonging to Bütschli's foam structure. This may readily be proven by observation and experiment. But besides such phenomena, I find in the living substance others which not only cannot be directly grouped with them, but which even deny the possibility of such an explanation. There exists here another set of controls constantly disturbing and transcending, yet inseparably bound up with, arrangements and equilibrations urged upon the substance by the given physical foam nature.

[74] In other words: The vital phenomena of protoplasm were seen to be not so much manifestations of the visible vesicular form of the substance, as upon, or through, this.

(a) The most important phenomena of the living substance are really to great measure independent of the visible foam structure. I find them to be referable in all cases to activities of the continuous substance of Bütschli's structure, and to like activities of the continuous substance of the finer foams.

(b) In most cases they can be seen to pertain wholly to the interalveolar stuff, and it is to this as organized, living, substance that we must look for the clue to a bewildering labyrinth of phenomena and possible interpretations.

(c) In any visible foam structure, negation of such physical controls as have been formulated for protoplasm, is always expressed by the continuous substance, or is always to be directly referred to it at any given moment.

[75] Perfect as may be the structure of Bütschli, or even a finer foam, in any area; stable as it may seem in any protoplas-

mic mass; there is thus given no true assurance that the living substance is at rest. Mass pellicles, alveolar layers, and, within these, area upon area of structural differentiation, may lie seemingly unchanged from minute to minute, or from day to day, or even throughout the rest of the lifetime of an organism, after they are once formed; and still a continuous train of substance activities go on, resulting in formation of new structures, both within and without the mass.

The coexistence of a stable and perfect structure of Bütschli with a host of metamorphosing activities of the substance as such; this forms one of the strongest reasons I would urge for preferring optical research upon living material to more indirect methods.

[76] The continuous substance of Bütschli's structure seems to be very active in all organisms observed. It is indeed most commonly in a state of flux, or of active contraction. Sometimes the two states are found to exist interchangeably in the same area which may be stably organized, even for contractile purposes, as in the cuticle of Vorticellidæ, or the delicate skin of rotifers. In pellicles, whether internal or external, excepting those which have been wholly altered by deposit of mineral substance, or chitin, or the like; no matter how stable and persistent their seeming under inadequate powers, no matter how stable as such the structure of Bütschli underlying them; there are evidences at one time or another, or at most times, of a more or less active flux, or of contractile displacement. Areal, or mass, viscosity so great as to produce considerable resistance to mechanical tension or pressure, seems no bar to unrest of the continuous substance.

(a) Alveolar layers and many other areal organizations of the substance are constantly intermitted, or broken up, by such instability of the continuous substance, which is comprehensible only through knowledge of its finer foam structure. In the finer structure itself is again repeated the same set of phenomena,[1] so that it is plain we cannot stop even here satisfied with foam structure as an adequate explanation.

(b) The motion of the "granules" upon the surface of very

[1] See filose phenomena, cilia, etc., below.

stable areas of Bütschli's structure, their transportation from place to place in the meshwork, and certain marvellous filose displays from the surface of stable pellicles covering stable arrangements of Bütschli's structure, are thus explained; also those phenomena seen in masses and extensions of protoplasm whose whole bulk is less than the thickness of interalveolar substance in many an area of Bütschli's structure.

(c) The Brownian-like movements of granules and vesicles in fluid, living, protoplasm at times,—notably among the Infusoria during certain states correlated with reproductive phenomena, when the nuclear bodies are broken up into fragments or granules, may doubtless be referred to this cause.

(d) The formation and the dissipation also of larval areas and organs are, as will be shown, due to such activities of the interalveolar substance; whether secondarily or primarily is yet to be determined.

[77] The flux and the contractions of continuous substance are a cause and a means of displacement of protoplasm, not only in bulk internally to the mass and also along lines of the meshwork and pellicles; but outside the mass or area into the water or other environmental substance.

[78] Displacement of this latter sort, which at times involves a relatively large proportion of the protoplasm in a mass, may go on, yet be invisible except under specially favorable optical conditions, and, as will be shown, even under these. The displaced substance because of its minutely subdivided state may still remain invisible; and may later be returned to the mass in the same manner that it issued forth, while the observer is unconscious of any phenomenon except, perhaps, of change of bulk in the mass,—and for this, is there not always possible, and ready, a physical explanation of "osmotic changes"?

An instance of this may gain a little credence for this rather startling statement which will however be amply upheld in the course of these remarks. About a large Myxomycete, under observation for sequence of protoplasmic movements, the water was seen to swarm with granules and a vague suggestion of a watery material which was in places somewhat flocculent and was at first taken to be excreted substance. Doubtless it would

fall under the term of "slime" which is so freely used in connection with the Protozoa. The granules showed motion, but this was for the moment assumed to be "Brownian," or to be caused by currents from the pseudopodial flow of the mass.

After some moments' absolute rest for the eyes, increased illumination, with better adjustment of the draw-tube, and also some specially fortunate atmospheric conditions, revealed the truth. The creature was surrounded by an evanescent, Gromia-like network of protoplasmic spinnings, in the filaments of which the granules were held. It was the ever-varying position of the protoplasm of this network carrying the granules, which gave with insufficient powers, the effect of dissolving watery substance mingled with granules in motion. The network was in ceaseless flux of form and substance, yet the flow and motion of the organism was in no wise altered from its characteristic manner and appearance by these peripheral phenomena. With very little alteration of optical conditions, the whole set of external phenomena would disappear like a dream, and one would see as usual the seemingly smooth and viscid surface of the heavy lobose processes and network. From time to time the spinning phenomena were locally intermitted, the substance returning wholly into the general pellicle, there to be indistinguishably mingled with the peripheral protoplasm, and so, after a while, to return to the endosarc.[1]

In the face of facts of this nature, it is difficult indeed to hold to any faith in surface tension as an adequate explanation of the protoplasmic flow. And these facts are not exceptional; they are peculiarly characteristic of the living substance where-ever its more secret processes can be traced.

While Bütschli thinks amœboid flow proper to be physically explicable by surface tensions consequent upon the mere physical form and the argued chemical nature of the substance, he confesses with characteristic candor: "I find myself, despite my best efforts, unable to apply the same explanations to the finer formations, such as free filose formations, of which Gromia furnishes a good example."

[1] See also below, filose activities in starfish egg.

[79] It is these latter, the free filose phenomena, not amœboid flow, which I find to be most universal, most characteristic, and most fundamental in the living substance.

Amœboid flow is but filose flow organized over a sufficient area to include to some considerable extent the structure of Bütschli. Division between the two has been made on the arbitrary ground of difference in relative size and shape of the mass involved, and on acceptance of the structure of Bütschli as the final structure.[1]

Filose spinnings from pellicles are so frequent that they cannot be overlooked. To such cilia owe their origin, and it is noteworthy that they arise with equal freedom whether the pellicle be external or internal to the mass. Cilia are formed by spinning from a pellicle of Bütschli's structure, or from the pellicle of the finer froth. In the former case they are apt to arise just above the apex of each alveolus of Bütschli's structure underlying the pellicle, and there is a quite definite tendency to formation of alveolar layers beneath ciliated pellicles. Because of viscidity of the interalveolar substance in such layers, preservations give an appearance which observers have described as "microsomes," each supporting a cilium.

Where cilia arise from the pellicular substance of the finer froth, they are very delicate, and seem to clothe the surface of the pellicle evenly. In their presence it is not possible, because of optical interference, to see the finer foam structure, but from their number and evenness of distribution, as well as their distance apart, it is hardly rash to say that they bear the same relation to the finer alveolation of the pellicle that the coarser cilia do to the structure of Bütschli. It sometimes happens that the coarser cilia arise at points which correspond to union of the continuous substance with the pellicular substance. I do not remember a case in which the coarser cilia were scattered quite irregularly over a surface.

Cilia often appear to be formed by splitting up of an undulatory membrane. I believe this to be to great extent an optical illusion born of the simultaneous and harmonious action of many cilia beating in time, then changing to a rhyth-

[1] See Substance as Organism.

mic and wave-like alternation. This sequence of actions is common in cilia not only when first formed but after any resting period later. It is also possible that they are at first covered and bound together by a delicate film of protoplasm so as to form a striated undulating membrane, but even then they are already formed organs and filose products.

[80] The length of cilia was found in all cases to exceed that given them in published drawings. From the Protozoa to the Rotatoria, and from these to starfish and sea-urchin larvæ, rays, cilia, sense-hairs, and flagellate appendages seem to be longer than is figured, except in Messrs. Drysdale and Dallinger's researches upon the monads. This was evident to me years ago with no powers higher than a ¼ Crouch objective, but then it was supposed to be economy of space which had led to suppression of the total length. I am now inclined to think that these processes are not seen to their full extension by most observers, and there has been evidence in many cases that the finest extensions eluded my most carefully arranged optical conditions.

[81] Pellicles spin almost everywhere; and under very adverse physical conditions, as one would think. The interalveolar substance seems to be irrepressible. What more unlikely physical opportunity for such activity than from the inside of alveoli of Bütschli's structure? Yet this I have many times seen, even during strongly contracted states of an area, which meant great compression of the alveoli. And in coarser alveoli of fluid endosarc such extensions are not uncommon.

[82] The interalveolar stuff spins itself out also along paths within itself; that is, protoplasmic processes, like delicate heliozoan rays, are extended through the interalveolar foam, between the vesicles, just as such rays are often forced through gelatinous material of some considerable density surrounding a radiolarian. Indeed, the protoplasmic substance is found acting and reacting on and to itself, as if it were a true fluid environment. In this fact I find one of the strongest arguments yet given for accepting the vesicular nature of the substance.

[83] Cilia, fibres, and undulatory membranes are formed by interalveolar substance in the heart of unbroken networks of

Bütschli as freely as in the water by peripheral protoplasm. As soon as their structure is complete and their activities fully organized, they function as if in a watery environment, and the surrounding substance gives way before their rhythmic pressure as a fluid alone would do. And when these structures are from time to time returned by invagination to their native environment, the protoplasm again yields fluidly to their beat. It is after the manner of a visco-fluid that the living substance yields also to pressure of adventitious substances, and to that of internal filose activities along lines of the interalveolar foam, as well as to pressure of contorted muscle bands.[1] The changeful viscosity of the substance gives the necessary physical opportunity for such phenomena.

By such interalveolar activity are explained the seemingly independent motions of the "granules," and many transpositions of the nuclear elements. The motion of granules along, and also to and from, pellicular surfaces Bütschli found himself obliged to interpret by supposing the granules to be governed by local surface tensions, and to have in this wise an independent motion of their own; especially because these pellicular surfaces bounded stable and seemingly motionless alveolar layers of his special structure. This inference, although a logical one if that structure be accepted as the final physical structure of the living substance, can no longer be made in view of the facts given here, which establish that such pellicles are thick, and often compoundly viscid, foam structures themselves, in whose area can be repeated the chief phenomena characterizing the masses they as membranes limit.

That cell walls have a value in protoplasmic masses of mere areal arrangements of the finer foam is shown by countless facts, some of which are to be given below. It is certain that where cells are in close apposition, their walls become to great extent common to both, or all, such cells. Granules and even pigment, I have seen pass along the surface of adjacent cells, with evident disregard of any separation line between them as cells. Again, within the common mass of two fused cells in egg cleavage, in that area which is central to the mass

[1] See Striation — formation of aster rays, etc.

and which becomes rhythmically more fluid, I have even seen yolk transferred from one "cell" to the other. In fine, there are strong optical reasons for refusing to hold that the cell wall is a true isolator of portions of the substance in a mass, and for inclining to believe that the living substance may overstep them at times in its more intimate functions which as yet we cannot hope to trace fully.

Perhaps the most striking and significant cases of filose activity found were in the developing eggs of starfish and sea-urchins. Protoplasmic activities of the pellicular substance were seen throughout the normal development of starfish and sea-urchin eggs, notably the former. The phenomena were observed in two different species of each group, had from two widely separated localities in two succeeding years. Many camera drawings were obtained both of normal and abnormal eggs.[1]

The filose processes were in the main invisible except with the 2.0 mm. immersion with the 8–18 oculars.

The spinnings contained granules in their usual form, and also in their reduction form, when they were no longer visible except as a changed optical quality of the substance which then appeared quite structureless. The vesiculation of the processes was much finer, as a rule, than that of Bütschli's structure, and in the normal egg the extensions were wholly of the finer, pellicular, foam. In most other respects they were typically protoplastic, of a radiolarian type. The filose activities seemed to be continuations in kind of those which produce the tuft to receive the sperm in the sea urchin; and in starfish accompany extrusion of the polar globules. They arose from the general periphery of eggs before cleavage and thereafter from the whole periphery of each cell as fast as it formed, ceasing only where and when cell surfaces were again fused with one another.

The activities were maintained in normal eggs by pellicular material alone, or by this reinforced from underlying, interalveolar, material. That it could be as last stated was manifest in

[1] As I have recently published in the JOURNAL OF MORPHOLOGY a detailed account of these phenomena, I will refer the reader to that article for fuller accounts of many facts more briefly passed in review here.

abnormal eggs where the excess material came, it was plain, from an underlying structure of Bütschli, which might be largely involved if the egg's condition were markedly abnormal.

There was no true intermission, except very locally, at any time during development up to the blastula stage when the activities ceased externally to the mass for a short time, only to burst out once more as cilia formation. This organized manifestation terminated them peripherally, so far as I could see in following larval stages up to formation of the skeleton in three dimensions, or to formation of the proctodæum. To the end of my observations, filose activities persisted internally as delicate processes crossing the blastocœle and attaching themselves to its walls, to ectodermal processes, or to those of mesenchyme cells. For a time after gastrulation, the inner ends of the ectoderm cells were elongated, and the optically wedge-shaped interspaces so formed were crossed by strands and webs of filaments.

There was no intermission in the course of development which could be interpreted as sympathetic with karyokinetic rhythms, except a momentary cessation near and at the line where a cleavage split was to pass. Following in the path of cleavage as fast as blastomeres became split off from each other, there sprung up renewed spinnings. These filaments extended themselves, with or without ramifications and anastomosis, but always with markedly less of these phenomena than belonged to peripheral spinnings, until they first reached filaments, or the pellicle, of the sister cell which was being separated. Filaments between cells held, as a rule, a more direct course, ramifying less than those of the periphery, and having a tendency to structural reduction, seen finally as change of optical quality. These traits became more or less emphasized in them after their first attachment to a sister cell. Withdrawing their branches, several filaments would fuse longitudinally with each other to form bands, or bridges, rather than attached rays, of protoplasm between cells. At certain stages in cleavage the structurelessness and viscosity of aspect in these connections increased, that is, *at such time as the cells drew together again.*

The processes sprung up close on actual splitting apart of the cells, so that at no time was it usual for the products of a cleavage to be physically separate from each other, though with slightly less efficient optical conditions one could see no connection between them.

[84] Continuity was, in fact, hardly destroyed at any point of the substance in cell-division before restored by filose projections from both the sister cells.

The phenomena were more profuse in earlier than in later stages. In my most carefully preserved specimens I have obtained but a much reduced number of fine spin processes, and these were somewhat altered. No reagent, not even heat, is quick enough, nor can one be applied so quickly as not to give the sensitive living substance time to react. Even with greatest care such processes are liable to be withdrawn during killing operations, and further manipulation for sectioning is very destructive to these delicate formations which when living have the sensitiveness of end-organs and a rapidity of transformation almost equal to that of thought processes. On the other hand, the reader is earnestly warned against pseudo-filose threads and webs which seem to be caused by chemicals and section fixatives, — and it is not impossible that slow killing may stimulate cells to abnormal or unaccustomed spinning. A student must have large familiarity with such processes, not only as to habit and type of formation in normal living eggs, but as seen among the Protozoa, especially the Protoplasta, before risking predication as to appearances found in preserved or sectioned material.

That portion of sister cells which was at some moment internal to both as taken together, was usually last to become fused, and here the filaments could be longest watched.

Not only between sister cells of a recent cleavage did filose processes pass. In the four-celled stage, the central cavity was filled with a web of these filaments, as was also the space between the group and the egg membrane, where they were, as a rule, more delicate. In the eight, sixteen, thirty-six celled, and intermediate, stages, — for I find the cleavage to be by no means regular, as my text-books asserted, but to follow a spiral

order, — the whole group of cells continued to be surrounded, and bound together across the central cavity, by such processes as have been described. Constantly extended, or returning, to one or another of the group, it was often impossible to know to which cell a process belonged, or with which it would next ally itself.

[85] That such physical connection as is established by the filose processes is not physical only, is shown by passage along them from one cell to another, and even by a palpable interchange between cells, of both granules and granule-bearing substance. Since in certain eggs in the 8–16-celled stage, in which the cells had been induced by continued pressure to separate quite widely from each other while continuing their filose activities, the order of cleavage and arrangement of cells in the characteristic spiral was not changed, it seemed clearly proven that by the filamentous connections there was maintained true correlation and interaction of cells, notwithstanding a separation of their pellicular surfaces. The fact that such was the case was noticed and pointed out to Dr. Whitman long before I discovered the actual means by which the seemingly inhibitory conditions were transcended.

[86] The cleavage pore appeared to be closed by somewhat amœboid activities of the cells about it, and also by peculiar activities of the spinning sort. There were at times in the optical quality of the filaments those differences which characterize contracting matter.

[87] In early stages the blastomeres may at times be sensibly reduced by outpouring of filose processes, but except under favorable circumstances and very good light, the true cause escapes the observer. A film of dust, or moisture, or of grease from stage fittings, or even from the touch of the human finger, on the surface of the sub-stage condenser, is sufficient to obscure all filose processes.

Eggs on which a continuous series of observations were made developed into perfect free-swimming larvæ. Increase of heat up to a certain point stirred up greater filose activity without causing the general development to swerve from the normal. Beyond this point, which was not definitely ascertained in

degrees, the filose activities seemed to drain off the egg's energies and interfere with the course of development. If the greater heat were continued, great sheets and webs of protoplasm, nearly all hyaline, were given off; and later, the eggs, or cells, would be much distorted by displacement of even the yolk-bearing areas. Variable quantities of displaced protoplasm extended towards the membrane and adhered to this by means of processes along which more matter took its way. Immature eggs and eggs overfertilized seemed most prone to these orgies of spinning, and in instances quite forgot any cellular destinies in exhausting themselves by such fruitless activities. The immature eggs were most markedly abnormal in filose ways. Most observers have noticed a sort of shapelessness and even amœboid changes of form in such eggs. These protuberances are seen with highest powers to be but the base of great webs of filose activities. In mature and normal eggs the activities do not cause the slightest change of optical seeming, except that they emphasize, perhaps, the slightly granular look of the surface and may have been up to this time mistaken for such a condition.[1]

Even more remarkable from some points of view than the activities of the cytoplasm just noted, were those of the polar globules.

[88] From the moment of their extrusion the polar globules showed filose activities of their cytoplasmic substance, no less marked than those of the egg cytoplasm; and usually in more or less intimate connection with these latter. They retained these activities until time of closure of the cleavage pore when they were drawn, or migrated, inside the blastula, and there retained their social union with the ectoderm filaments until formation of the endoderm processes and, still later, of the mesenchyme web, when they could sometimes still be detected in union with this also.

Their chromatic substance preserved all the while a most sharply marked and characteristic optical appearance, though

[1] The fact that even in these strongly emphasized abnormal cases the spinning activities have not been described, points to the reasonableness of believing that the finer, less obvious filaments of the normal eggs have been overlooked also.

it was often separated in the form of granules and then again drawn together into a compact and nuclear-like mass.

In all respects these strange little masses of living substance looked and behaved like small protoplasts. Their webs and processes were ceaselessly extending themselves on all sides and becoming mingled and entangled with those of the cytoplasmic webs. The intercellular space above which they lay and which came later to be the cleavage pore was crossed and often well filled with fused, and interlaced and intermingled, spinnings from the polar globules and adjacent cells.

That the polar globules persist for a long time as active and seemingly independent substance, or units, was clearly shown. More there may be of even greater significance, seeing that they are again returned to the general mass of egg substance. Is it not possible that, as the cells have but a semblance of separation, these bodies also are but portions of the organism temporarily segregated for physiological purposes?

Protoplasm squeezed from eggs in the earliest stages spun more or less vigorously, according to the time in certain rhythms of viscosity of the cells that the experiment was made. Later, the filose phenomena were replaced by amœboid or lobose processes, or ectosarcal areas, all of which varied in their character according to the time in these same rhythms and in certain other rhythms which pertained to the whole development. With regard to viscosity of the substance in developing starfish eggs a number of very interesting rhythms were broadly noted.

In the single-celled stage, from the moment the egg is laid, there is a steady, progressive increase in peripheral viscosity of the mass, which gradually extends further and further inwards after the nuclear sac membrane is dissipated and its fluid contents distributed through the general cytoplasm.

After this, a quadruple set of rhythms of viscosity were noted in starfish and sea-urchin, also in rotifer, eggs. One set of rhythms held relation to cleavage of each cell, another to the whole progressive development of the mass. In addition to these was a double set of rhythms of varying viscosity in areas of the mass. One set held relation to position in individ-

ual cell-masses; the other to position, with relation to the whole mass of the embryo.

According to the point of time in each of these sets of varying rhythms, did the viscosity, elasticity, and resistance to pressure, of the mass or area vary; also the specific reaction of the substance when brought artificially in contact with water.

From the first it is true, that those portions which lie internally to the embryo as a mass are more fluid; and conversely, that the more peripheral portions are more viscous and resistant.

Internally to each cell also, whenever it stands separate, except for the filaments, from the mass, or its sister cell; there is always an area of more fluid substance.

After each cell again becomes firmly welded to the mass, or to its sister cell, that portion which is internal to the whole mass as then formed, becomes more fluid, without respect to the number of cells.

This seeming sensitiveness of the substance to its position in the common mass is the more remarkable since *the centre of the group is a cavity full of the same watery environment as surrounds the periphery*, because the conditions then would seem to be identical for all the peripheral substance, yet it reacts differently at different points with little or no regard to this.

In the four-celled stage, when the cells are sometimes firmly welded together for long minutes, there was marked fluidity of those portions, including the pellicular wall, which projected inwards towards the cleavage cavity. From this portion the filose processes extended, filling the cavity with a protoplasmic web. Yet the firmly knit and relatively very viscous peripheral portions were no less active in this respect. When a more fluid area comes in the rhythm to lie between two sister cells, the cell walls also share in the relaxed physical state.

[89] The viscosity of the substance is, then, rhythmically modified according to its temporary position with respect to external environment of the whole embryo; greater or less fluidity being assumed in the same region of a cell or the mass, according to its position as internal or external to that organization of the living substance. (See Substance as Organism—

Raphidiophrys elegans.) In the two sets of position rhythms it is plain to be seen that, while the substance controls its local state and structure with reference to external environment, this latter cannot be held to be the controlling factor, but only an influencing factor. Besides the above major rhythms, every smallest area of the cytoplasmic and nuclear substance seems to have rhythms of its own of varying viscosity; but the tangled maze of these it is now beyond our power to thread. They bear a constant relation to the phenomena of cell-division and karyokinesis, and are visible chiefly as local or strial modifications.

The production by protoplasm of a homogeneous, or ectosarc-like area, when it is artificially brought into contact with the water, was found to vary greatly, both as to amount and kind of such a formation, according to the time in the above complex set of rhythms in the area experimented on ; and to vary also in the peripheral substance, as such, from the internal substance, as such.

With regard to experiments made upon living substance crushed from protoplasts, in attempting to confirm, or disprove, experiments upon purely physical foams, it must be borne in mind, that, in the former case, the substance remains for a long time living, and in death disintegrates, so that we can not too readily assume a rapid formation by it of ectosarcal areas to be due to the same cause as the gradual formation of a hyaline peripheral area by the non-living foam ; basing such conclusion on an optical similarity between the two formations, which is in the main superficial.

That the formation of ectosarc by the living substance is not a direct physical result of contact with water, is abundantly proved by the fact that, in the same protoplast, from moment to moment, contact with water produces or does not produce ectosarc, excepting always a pellicle. Further there are in many protoplasts and higher Protozoa also, areas of most fluid substance, which on contact with water never form any ectosarc further than a very thin pellicular film. In *Amœba proteus* and *Amœba radiosa*, the ectosarc may be at one time only a film, and then again extend half across the body of the animal. It is frequently, also, formed within already existing

areas of ectosarc, the rush of substance transforming itself here as rapidly as when close to the water.

That ectosarc is not altogether a mere physical redistribution of the elements, but has reference to physical organization of these for physiological function, is manifest when one studies a transformation of ordinary, irregularly structured, endosarc into beautifully organized and uniform ectosarcal areas, in which are then seen organized contractile activities. Such phenomena can be followed from moment to moment in *Amœba radiosa*, where the endosarc can be seen to transform itself in a short time into ectosarc of mixed structure; this to pass into a manifestly organized state, and then into contractile states, in which all structure may or may not disappear from sight, the substance becoming so dense and refractive as to fairly glitter, and so resistant that when it has the form of long lash-like extensions they may be bent elastically by pressure as if they were bristles, and then in another moment will lash themselves about like the flagella of *Heteromita* or flow like the pseudopodia of *A. proteus*. In such viscous states in *A. radiosa* when a posterior mass has a thick ectosarcal covering, I have seen this thrown by contraction into folds which were so refractive as to simulate quite well spiculæ of flint, and by these contractions the whole mass, including an anterior, film-like, ectosarcal flow, seemed to be urged forward. In another moment the creature was a large fan-shaped film of protoplasm, so delicate as to be scarcely visible, preceding a protean, partially naked, lump of somewhat filose endosarc.

In addition to the facts cited and others of kindred import, negation to any explanation of cleavage by surface tension was had early in the summer of 1893 by the following experiment. A starfish egg in the two-celled stage was gradually compressed until the pellicular wall was broken and the peripheral protoplasm exuded at points from both cells, forming very short blunt processes. Little by little these were augmented by outflow of hyaline interalveolar substance, and at the same time they showed local changes in structure, and amœboid activities, the substance flowing here and there and spreading itself out over the surface of the whole egg. There seemed to be a

ceaseless series of these activities going on for hours, the substance heaping itself up here and there in lumps, and then again forming papillose processes over wide areas, and again, a thick, smooth pellicle.

Little surface tension for the mass would seem to persist under such conditions. As a matter of fact, the peripheral pellicle itself relaxed in places, extending its substance no longer in filose processes but in amœboid lumps, or knots, or films. Yet, all the while, the phenomena of karyokinesis and of actual cell cleavage went on ; more slowly than in normal eggs, but still without pause. First into four, then into eight, then into sixteen cells did the mass divide, forming internally perfect walls for all the cells, though there never occurred any actual separation of these from each other. Still, in the usual acceptation of the term, the cells divided ; that is, their mass was subdivided by, so-called, cell walls.

In the ectosarc formed by the egg substance after being squeezed into the water, structural reduction, and then in some cases, a reappearance of Bütschli's structure, were observed. The finest vesicles which could be detected showed no change of contour, so that here, as in protoplasmic ectosarc, a structureless appearance could hardly be attributed to mere stretching of the alveolar lamellæ, especially as the meshwork became often thicker and optically more conspicuous, rather than more tenuous and less obvious as reduction went on.

When pressure was applied to eggs in 4–16-celled stages, in which the cells last divided were still optically separated, filaments connecting the cells were seen to become thicker, denser, more refractive, and yellowish in tone. At the same time, if the pressure were slow, the viscosity and resistance of the cell mass also increased; and the cells showed a similar change in quality of their pellicular stuff, while many peripheral processes were withdrawn.

Rapid, or sudden, pressure effected a separation of the cells more readily, but seemed to be followed by the same optical changes in the cell protoplasm. If actually separated, but without rupturing the membrane perceptibly, as was done a number of times by pressure of a mixed rolling and squeezing

nature, the cells passed soon after through a great change of viscosity, visibly relaxing. They then showed rather marked change of contour, and afterward renewed their spinnings until once more connection was reëstablished amongst themselves, when by degrees they drew more and more closely together until they touched. The walls then coalesced and the two, four, six, eight, twelve, or more, cells were again a solid mass. After such coalescence there came on always a marked increase of viscosity in the whole mass, and markedly greater resistance to pressure. Just before renewed division this would again be somewhat relaxed, and the spinning phenomena more active.

During the past two years I have observed in the blastomeres of frogs' eggs the same increase of resistance under gradual pressure, and similar changes in some few of the lobose bands of protoplasm or ectosarc by which, when separated, they had restored connection.

[90] There can hardly be a doubt but that there is here shown a definite physiological resistance to certain adverse mechanical conditions in environment; that the living substance responds in character of its own powers to stimulus of a given sort; that this response is to conditions which are probably new to the substance, and is, moreover, contrary in its nature to that given by purely physical foams.

For, had the substance thus dealt with been an inert, purely physical, foam, bridges and bands of it connecting the cells would have shown a most contrary series of reactions. Under pressure that forced apart the cells, they would have become more tenuous and longer, as well as less distinct and less refractive optically, and the pellicular substance also would have become stretched and less refractive. The peripheral processes would have been increased in length and mass, and also, no doubt, in number.

The phenomena of the living eggs were on the other hand exactly such as characterize all protoplasm, whatever its form or position, in contractile states and especially during active contraction. Further proof that this was actually the case was given during the usual drawing together of separated sister cells after cleavage was ended. First the cells usually rounded

themselves up on all sides, except those of the cleavage plane which were connected by filaments. Finally, after a number of changes of form, these sides, which were then rather flattened, approached each other more and more, while the protoplasmic bridges showed greater homogeneity and even structurelessness, with increase of viscosity and refractiveness. They thickened too, in many instances, as the cell surfaces drew together, until at last the pellicular surfaces were too close to admit of further observation.

In sea-urchin eggs, the spinning phenomena were fundamentally the same ; the filose processes, however, were less profuse and finer. Similar varying rhythms of viscosity, and flux of pellicular and interalveolar substance were also observed. In this form the segregation at certain rhythmic intervals, or rather in certain rhythmic progressions, of pigment granules from certain portions of the cytoplasm was interesting and suggestive, not only in connection with a flux of continuous substance along lines of the meshwork and pellicles, but as correlated with structural preparation of certain areas for specific physiological function. Before each early cleavage, pigment granules were carried along the pellicles in a flux of substance towards the line where the split was to take place, and appeared to be carried onwards and inwards from this point, but about this last there is yet some doubt in my mind.

In rotifers' eggs a similar segregation of yolk is extremely marked, the very planes of cleavage being thus for a long time clearly indicated before there is any other sign of an order of cleavage among the cells.

Such phenomena are thoroughly in accord with the general habit of the substance in withdrawing interalveolar substance to an area where its activities when organized will not be hampered by inelastic, or irregular, inclusions ; or of withdrawing the inclusions to another place. The areas cleared of yolk in segmenting eggs are noticeably areas in which are about to take place organized contractile activities, as amphiastral areas, or cleavage planes.

Pigment, yolk, and granules are carried thus in instances from cell to cell. Flux of interalveolar and pellicular substance

can be traced often by movements of such inclusions. That cell walls form at times no barrier to wanderings of the living substance seems to be shown. It is noteworthy that these things can take place without disturbance of a structure of Bütschli.

Since these observations were made, there have been many additions to our knowledge of intercellular connections in higher Metazoa. They are but links in an endless chain of evidences that the living substance clings pertinaciously to its protoplastic habit; and that the formation of a firm peripheral pellicle about subdivisions of a whole mass is in any case no proof of actual physical, or physiological, separation of the substance, any more than the presence of stable structures of Bütschli argues a quiescent state of the living substance.

I am aware that, because of the restrictions of the preserved and sectioned condition in which most intercellular connections have been discovered, these are commonly regarded as stable processes from the cells. I think we have now grounds for thinking of them as possible routes of travel of the unstable and migrant substance, or at least as protoplastic formations. For everywhere I find the living substance shifting its whereabouts, combining and recombining its elements, and always, after each turn of the physical kaleidoscope, there is found associated with the new design a new manifestation of ordered activities.

Clearly it is a habit of the substance to be tenacious of continuity between portions of its mass, except when it organizes its activities and itself to transplant a portion of itself to a new environment.[1] Those apparent contradictions of this fact offered by blood corpuscles and wandering cells do not interfere with this view since in the case of the latter, and indeed all cases in which exist protoplastic activities, there is reëstablished from time to time by means of these a true connection with the areas of viscid foam through which they wander; and in case of the former, a slight readjustment of our standpoint, or even a slight addition to our knowledge of their true life history along the lines of these studies, may bring them strictly within the same assumption.

[1] Fosterhood.

[91] The true nature and mode of formation of cell walls seem to be that they are but pellicular modifications of the continuous substance of masses into plates, or membranes, which are as readily formed internally as externally; that they do not differ either in origin or constitution from other internal and external physiological pellicles or ectosarcal formations; that they are, in short, not substance dividers nor substance isolators, but *substance structures, substance differentiators, and differentiations, substance organs; and finally, that they belong primarily to the mass and but secondarily to cells.*

[92] We can no longer regard these formations as having for the living substance the value of a prison wall. We must rather look upon them as *substance strengtheners;* as devices for securing a qualified independence for areas which yet maintain absolute physical and physiological continuity. They limit to some extent the areas surrounding centres of control distributed through the mass. By such "centres" I mean the nuclei, which would seem to control the supply and the use of specific environment of the substance as such.

The pellicular membrane which surrounds cells is no better reason for thinking of these cell areas as isolated, independent, *reproductions* of the original unit, than is the nuclear membrane for calling that organ an intra-plasmic cell.

[93] Notwithstanding this reasoning, Metazoan development may still remain to our thought a multiplication of cells, but must cease to be to it, as of old, that multiplication of morphological units which Huxley preached. *It is rather subdivision of the substance, with or without growth of mass, than a reproduction of the first egg cell. Cell division is mass differentiation; that is its true meaning,—making it one with all the host of substance organizations of the elements of the living substance for physiological function.*

Passing in review in the light of all my facts those colonial and compound organizations of living substance found in both Protozoa and Metazoa, it becomes evident that so long as there is between the units composing it, a protoplasmic connection, even the most delicate, a whole colony must be conceded the value of a morphological unit, and each so-called cell, or unit, of

the colony must be looked upon as merely an areal organization of the substance of the whole. For there is no true difference between a connection such as is shown in Vorticellidæ, where the contractile stalk of each unit is continuous with all the others by way of a common or multiple stem; and that seen to be established in a compound Heliozoan, or compound Cœlenterate, or even in a developing starfish egg.

It seems strange that Huxley when he had been led to declare for the compound Cœlenterates the value of true morphological units should have missed the unity of such a relation throughout the living kingdom.[1]

[94] To sum up very broadly what has been shown of the activities of the living substance: these have been seen in all cases observed to be correlated with an ectosarcal arrangement or organization of the two groups of protoplasmic elements; and they have been seen in all cases to transcend any visible structure. In other words, the activities of protoplasm are not to be directly referred to, or accounted for by, any structure we can resolve by our present optical resources.

[95] Further, all visible structures have been seen to be a direct result of activities having the same character as those seen to be inseparably correlated with the visible foam structure; that is, visible structures are the direct result of activities correlated with a finer and not visible series of kindred structures, in which we are constrained by the evidence to believe the same relations of living substance and structure hold good. Thus any explanation of the activities by structure is removed beyond our present reach.

[96] Last and most important, the visible structure of organisms, of organized masses of the living substance, was seen to be relative only; that is, the areas exist in relation to each other and to the organism as such, while the living substance in great part ignores these visible fixities, circulating freely beneath the mask they form for us. In its more secret life protoplasm is unstable and protoplastic, however rigid the structural forms it maintains. The form persists — the substance composing it is not fixed at any point in it.

[1] See Substance as Such and as Organism.

True protoplasmic life and habit lie hidden beneath those very forms and habits of a grosser nature in which they have hitherto been sought; as too often happens, the oracle has been veiled by the very terms of its expression.

In those sections which follow after Contractility, many more facts are added and this line of thought is further expanded by their means.

STRIATION.

At the outset of this record of facts, I should like to disclaim any attempt to deal as one who knows their conditions and limitations, with the great problems of molecular physics involved. Bütschli has proved upon his artificial foams certain physical forms and interactions, and applied these in his researches into the phenomena of the living substance. I have ventured no more than to extend still further along the same lines the same set of comparisons, using however certain other phenomena which escaped Bütschli's observation, and seem not to have been recorded at that time for his criticism.

In supposing that I might follow so far as he essays to take his readers, I may have been misled by the very lucidness and thoroughness of Bütschli's analysis and demonstrations, so far as these go; and for precise understanding of them I have depended to some extent upon the authorised English translation by Minchin.

Bütschli found that a linear arrangement of alveoli, in both fluid and very viscid foams, produced an optical, or what might rather be called a psychological, striation of the substance. He has shown that this effect is given also where the alveoli, in addition to this purely mechanical arrangement, are elongated in the same direction by compression, or osmotic changes, or by tension of any sort causing extension, or stretching, of the lamellar material. He finds himself able to group under these heads all optical striation of the living substance, and he expresses himself to the effect that a fibrous appearance depends solely upon the arrangement, or extension, or stretching, of the meshes in a given direction. Irregular, and tangled, fibrous structure, can always, he thinks, be explained by the fact that

at these points simultaneous or successive strains took effect in different directions.

Here as elsewhere I find that Bütschli has laid down an impregnable basis of fact. I find optical striation to be, as he asserts, associated always with a distinctly linear arrangement of the meshwork substance of a vesicular structure. I find striations like those he describes as typical in his artificial foams, are plentiful and can readily be found in living protoplasm. It is easy to produce them also in almost any area of the living substance by simple compression, or extension, between cover and slide. The best results are to be had in areas quite but not too viscid.

I find, beyond this, that there are many conjunctions of circumstance which constrain or impel the mind to strial interpretation of an optical network. Some of these seem to be very slight causes, one would think, but the ever too ready mind receives impulse from them, nevertheless, in one direction rather than another, and, moved by such slight matters as relative size, or even difference in geometrical shape, of vesicular contours, hastens here or there, shaping lines of emphasis for itself. The accustomed haste of its movements, being now under the spur of enforced attention also, strengthens such an impression, and may conduct the eye in tortuous or broken curves, as well as in more or less straight lines. In some areas, influences such as these urging the mind simultaneously along a number of paths in a given plane, contend with each other, and so produce an aspect of tangled fibrous structure.

To hold well in leash, without unduly restraining, this eager poise of the mind; to protect it as much as possible from the vitiating habit of predication which ordinary education and human intercourse teach; these are some of the most necessary and most fruitful lines of self training for those who seek to know the living substance as such. Where the mind follows within the limited depth of focus of the high powers used, it selects from amongst the fused lamellæ of the very irregular polygons which at times represent the foam structure, the most obvious and connected paths or lines of the continuous substance; and a falling of these above or below the plane of an

optical network, makes such false striations which really have little to do with the true and common structural relations of a strial sort. In sections, a tearing, or displacement in shrinking, of the visco-fluid lamellar substance may cause a marked, but false, seeming of structural striation. However strongly meshwork lines extend in a given direction, caution must be used in inferring tension, by osmosis or what not, in that direction, for a marked, and seemingly simple and direct, striation in one optical plane may express diverse strains in other directions.

In tracing many optical striations of protoplasm along lines of, so-called, optical emphasis, I presently became aware that besides these were others of a different origin and nature, having marked specific characters. Here too it seemed that though a true word had been spoken and a strong word, yet, as in the case of the foam structure, it was not the "master-word" of the situation. Comparing the new sort of striations with those just described, it seemed to me that certain definite physical, and psychological, or optical, qualifications of these latter did not apply to the former. If I am mistaken in supposing these not capable of being grouped with products of purely physical, or mechanical, lamellar extension, the physicists will not leave the error long uncorrected.

Such striations have a basis of actual physical difference in mass and character of the continuous, or interalveolar, substance, which causes them to have marked optical emphasis. Many of them were correlated with contractile activities, and were found to depend not only upon a characteristic passive arrangement of the continuous substance, but upon intermittent, or rhythmic, states and physical modifications of this. These were manifested optically by rhythmical, or intermittent, changes in its mass, density, refractive quality, viscosity, and position in the mass, or area. Striation may exist before and after contractile function, but the latter always produces in the substance either optical striation of a visible structure; or optical changes which are to be correlated with a similar structure beyond our reach; or increased emphasis of an existing striation.

There is another striation which may exist without being associated with organized contractile function; this is a local

difference in mass, or quality, of the continuous substance. It is often due to its interalveolar filose activities, but may result from more stable local increment where the interalveolar foam has a secretory or irritable function.

Contractile striation, and even true fibrillation, appear sometimes in very fluid areas of protoplasm. Then alveoli will be drawn into line, for the moment at least, along the course of the optical striation. Many swift and evanescent contractions of the fluid substance in protean forms or areas can thus be traced, and causes and means of motion of the protoplasm of amœba and kindred forms can best be seen and followed.

The line established by a contraction wave may be very tortuous among the vesicles, and thus bring into line, by, or for, organized action, those which were at first quite far apart. The converse is obvious, and the value of such a method in forming compound areas having enormous extension powers in given directions must be great.

It has already been stated that, from time to time, in areas and masses, the living substance varies its viscosity, and hence its optical qualities, becoming denser and more refractive when viewed with powers too low to resolve structure. In examining such protoplasm wherever possible under powers adequate to resolve all, or part, of the foam structure, the physical modification was found to be due to like qualities in the continuous, and chiefly in the interalveolar, material of the visible structure, irrespective of size, or character of arrangement, of the alveolar inclusions of Bütschli's structure. And the continuous substance held these characters for just so long as the area, as a whole or locally, held the optical characters noted. And wherever, under high powers, the interalveolar substance showed such characters in any area, however small, that area under lower powers had a marked distinctness and refractive quality which were persistent, or intermittent, in sympathy with the same character in the continuous element.

Further, those parts of the continuous element which had more marked refractive quality, were visible as distinct structures under powers which showed nothing of the rest of the network, however one might isolate minute portions for examination.

Conversely, wherever there were seen such refractive portions of lines of continuous substance, I either found directly by change to higher powers, or, where the limit of magnification had been already reached, was able to argue from other activities of the same area, or from associated optical phenomena, a true foam structure.

It frequently happens that there is an alveolar arrangement linear in two directions, and that parallel lines of an optical reticulum cross each other at sharply defined right angles, or at equal angles of other sorts, yet in these cases there may be true and very marked strial emphasis upon one set only of these lines; or may be upon both in alternation; or equally upon both, being in this last case markedly different from surrounding optical network lines also caused by linearly placed alveoli.

In both Protozoan and Metazoan groups, striations associated with contractile activities appear singly, and in simple or compound groups. Even so comparatively simple a form as Vorticella has a footstalk in which I find no less than five different areas of organized foam structure grouped in physiological alliance, each bearing some special part in the contractile activity; and there are indications of even more such differentiations beyond our reach.

It is often impossible to resolve with striations, cross lines of an alveolar network, simply because the striæ have been made visible by increase of mass of the interalveolar substance, — with increase also perhaps of its refractive power along those lines, — in a vesicular structure whose lamellar substance, without such increment, were far beyond our reach. Sometimes also, striations coincide, not with an optical reticulum of the plane in observation, but with that of a plane at right angles to this. Such a case was found in the cuticle of *Stentor cœruleus*.

If strial or fibrillar appearances of contractile areas, as correlated with physiological function of the substance there, are grasped in relation to Bütschli's structure, it becomes possible to understand how these results apply to phenomena found in the finer structure.

As a typical instance of contraction organized on a basis of Bütschli's alveolar structure, I will take the cuticle of *Epistylis*

flavicans, which has been variously described from time to time. Earlier observers thought the cuticle to be decorated with a beaded formation in the peripheral protoplasm. Greeff later ascribed the optical appearance to two sets of muscular fibrils surrounding the creature and crossing each other more or less at right angles. He thought that these two sets of fibrils contracted alternately as the animal extended, or shortened, itself.

I find the true structure to be that of a large cuticular layer of vesicles of Bütschli's structure, quite uniform in size, and covered by a pellicle of protoplasm which in its turn shows a peripheral layer of delicate alveoli of the finer foam, (now for the first time described). The interalveolar substance of the cuticular layer is much modified from mere lamellar substance. It contains strands, or plates, of the finer foam, which pass rhythmically from viscid to fluid states, showing from minute to minute a host of local, intermediate states and modifications of its structure. Such modification of the interalveolar substance is along lines in one plane, and in two directions. The lines lying between the alveoli intersect each other at such angles as the shape of the body directs.

When the animal was in medium extension, the optical striation was about as marked in one set of lines as the other, in neither so marked as during more extreme change of shape. The effect was then somewhat strongly that of the muscular fibrils Greeff described. If greater extension occurred, that set of lines parallel with the increasing diameter grew thicker, and gained in optical emphasis. At the same time, the other set of strial lines, running parallel to the decreasing diameter, lost optical distinctness by becoming thinner and thinner as extension proceeded. When the animal contracted, the phenomena were reversed. But still the loss of emphasis was always parallel with the decreasing diameter; and gain in optical and physical definiteness was always parallel with the increasing diameter.

If Greeff's idea were the true one, and the striæ represented two sets of muscular fibrils, quite another set of appearances would be seen, for then those striæ corresponding with the

shortening axis of the body would thicken as they shortened; while those having a transverse direction would of course thin as they elongated with the mass. The alveoli too, would then become more widely separated as the fibrils shortened, and would draw nearer together as these elongated. But it is just the converse of this that I found to take place in Epistylis, — for there the alveoli approach each other along the shortening, and become more widely separated along the lengthening, fibrils.

If we attempt to explain the phenomena simply by change of shape of the alveoli under tension stress, as in Bütschli's tentative hypothesis of contraction, the conditions exacted are just those needed in Greeff's explanation, and hence cannot be in place here. Especially are these things true, if the presence of the finer foam be taken into consideration, as indeed it must, for, during relaxed moments, the interalveolar substance showed filose phenomena, extending itself into the inclusions of Bütschli; the alveoli regained locally more rounded contours during general contracted states; and the strial substance even split into strands, or became visibly, though very minutely vacuolate; and during local contractions in these strands the alveoli slipped slightly along the striæ, or had their optical network drawn into triangles, or other figures.

Closer observation showed that the increased emphasis in the striæ was due to an actual displacement of interalveolar substance during contraction. During displacement of the mass in any direction, the interalveolar material forming the last emphasized set of striæ was in great part displaced, the displacement being an actual one, and following, as it seemed, lines of least resistance between the yielding alveoli filled with fluid; which may be prepared paths. The contraction wave which urged forward the substance, drew together the alveoli, and as the activity had the usual wave-like progress, the cross striæ became progressively increased in mass by access of interalveolar stuff. The ectosarcal mode of organization of the elements as typically seen in this cuticle of Epistylis, and which is characteristic of all areas of organized

contracting substance, is now seen to have manifest physical advantages for such a set of physical changes, controlled by contractility.

These phenomena were found gradually to be a key to a whole host of contractile phenomena of the living substance, as seen in optical changes of a visible, or inferred, vesicular structure. All apparent contradictions were found to fall under the same explanation, when based on the finer structure of the interalveolar substance itself; wherever the continuous substance in contracting areas was seen to thin as it elongated in sympathy with mass extension, and to thicken in sympathy with contraction, it was found to be itself the organized foam, or area of contraction. That is, the surrounding substance bore but a passive part in the contraction phenomena, and the striæ, if there were more than one, acted in harmony but without that structural dependence seen in the Epistylis cuticle. In such cases, then, the structure of Bütschli, or the visible organized structure, was not the active basis of physiological function.

In the highly elastic cuticle of certain rotifers, Philodinæa, where there is a beautiful organization of the elements as in Epistylis, it was noticed that striæ, after becoming, as in Epistylis, thicker and more obvious until the alternate set of lines was almost obliterated, then began to grow thinner and still more highly refractive, while extension of the mass and of their length continued. In other words, the limit of displacement of the interalveolar substance upon a basis of Bütschli's structure being reached, extension was prolonged upon a basis of the finer foam; the strial substance then functioning as true fibril.

All such cases, whether stable or intermittent, or only occasional, fall under the head of *muscular fibrils* of the substance. There are areas whose structure superficially resembles that found in the cuticle of Epistylis, which yet are formed of these independent, but allied fibrillations. I have found such in forms nearly allied to Epistylis. Single fibrils of this sort when they lie in areas of rather fluid, vesicular structure, slip easily in their extension or contraction through

the surrounding foam. They are not as a rule bordered by true lines of alveoli, and may lie in areas whose inclusions are often heterogeneous and irregular in size. They are independent of organization in the surrounding structure of Bütschli, or other visible structure, because they are themselves the organized contraction areas. By their contraction they can bring together separated areas, or cause change of shape in the areas they traverse, for they are commonly attached at their extremities to some pellicular formation, with whose substance they are continuous. They frequently become tortuous, or even plicated, in line during contraction, a phenomenon seen also in membranes, or in complex muscular fibres.

They may arise suddenly in areas where the interalveolar substance has been up to that moment markedly fluid; and they may again return, after a variable time of function, to the same state; such metamorphosis being accompanied by those optical changes characterising ectosarcal organizations and redistributions of the elements as seen in Bütschli's structure.

Returning for the moment to striation associated with contractility as an optical phenomenon of the substance, and laying aside the distinction between striæ and fibrils, the following variations were noted.

Strial emphasis may involve all, or a part only, of the continuous substance, and may or may not involve the walls of adjacent alveoli; therefore a marked striation may be bordered by spherical, or nearly spherical, alveoli which, even during active contraction of the strial lines, may not change their form.

Striæ in living protoplasm may be in number independent of the number of rows of alveoli amongst which they lie.

Their thickness varies greatly in different instances, as well as intermittently, or rhythmically, in the same series from moment to moment. Compared optically with the rest of a given reticulum at such times, they are like cords or strands of a different constitution. Isolation of small portions of their length shows them to be a physical differentiation, and mechanical experiment shows them to have a definitely resistant and often highly viscid consistency.

The length of striations varies to any extent, and may do so independently of a quite stable linear arrangement of vesicles along their course. It will vary in a series or in a single stria from moment to moment. Striæ may lengthen or shorten rhythmically or intermittently. During shortening they may become more tenuous, delicate, and finally less viscid and refractive, and even disappear from sight or from all but the closest scrutiny. Or they may become thinner and more obvious optically, because more refractive.

They may become thicker and more refractive. Those striæ which I have distinguished above as true fibrils, become always thicker and more refractive during shortening contraction, and thinner and more refractive in extension. But striæ may lengthen actually by implication of new substance and not by mere displacement of already organized substance. They may shorten likewise by relaxation of such organization along lines once emphasized. In other words, the physical conditions in the finer foam on which they depend may be as unstable as similar organizations in the structure of Bütschli. Such phenomena as these latter are best seen in the development of eggs, where the elements are constantly undergoing metamorphoses of structural arrangement.

Striæ may travel from place to place without visible disturbance of an existing structure of Bütschli, or arrangement of its elements. In such case, they progress either as a wave of influence upon interalveolar substance, or as actual displacement of this along interalveolar lines.

It is common in contractile tissues, or areas, whether stable or unstable, among Protozoa, and also Metazoa, such as hydra, rotifer, frog, and starfish and sea-urchin embryos and larvæ, to find ladder-like arrangements of the vesicles, of various lengths, extending in a number of directions with respect, not to a common centre, but to many centres, and as it were growing out of each other at various angles; the optical or linear emphasis beginning or ending at any point, with or without extension of the alveolar walls of the structure on which it is marked out. A kindred incoherence of divergent emphases may be seen in the unsegmented egg of starfish and

sea-urchin and rotifer eggs before the protoplasm reaches a more uniform arrangement preceding first cleavage. In some living epidermal cells of a small marine fish, I have found a curious *whorled* effect produced by the interalveolar substance lying in somewhat concentric but branched lines, these controlling the form of the network to such an extent that the optical reticulum was in places triangular; yet closer observation showed that the vesicles themselves had true fluid contours notwithstanding. As pathological states set in, preceding death of the cells, the concentric, or whorled, arrangement gave place to a more and more regular and even structure of Bütschli, the relaxed continuous substance becoming less obvious, the vesicles swelling very perceptibly and their hue changing also to a darker and bluer tone. This by lamplight.

In transversely striated muscle bands in a rotifer, I have seen coarse striæ which were visible in states of medium extension, separate during greater extension so as to become resolved into double striæ. Between these, vertical alveolar walls could be seen at happy moments of optical conditions. At first only each alternate stria would so separate, but in rare and extraordinary extension of the muscle band the other alternating striæ would half reluctantly separate also, and show their structure to be the same. Here were evidently reserve powers of extension and of elasticity.

The rapidity with which the elements of a given vesicular structure can be re-organized for contractile activities, is a very important point which must not be passed over. If I say that such can take place "in the twinkling of an eye" it may sound like exaggeration, yet such is indeed often the fact. Of course where an existing structure of Bütschli remains unaltered, the contraction is referable to the ever present ectosarcal nature of the continuous substance, having ready prepared just the structure for organized action of the substance to take place in.[1]

[97] Cilia are truly but external striæ, both as regards their origin and mode of formation.

Most remarkable are the phenomena of the aster rays in

[1] See Substance as Such.

starfish and echinus eggs, first observed by me in 1893 at Wood's Holl, when they formed one of the strongest incentives to these researches.

Bütschli ascribes aster appearances in segmenting eggs to an optical effect of linearly placed and stretched alveoli, and to illustrate this, has figured a cross section of a preserved sea-urchin egg, showing in the "attraction sphere" an indubitable radial and linear arrangement of the vesicles. While an optical striation is undoubtedly produced by the condition shown, I am unable to identify this with the appearances of the living egg; and it is surely impossible to explain thus other phenomena seen there. In the "attraction sphere" as figured, radial increment of substance is compensated for by increase of size in the alveoli whose walls form the striæ; in the living egg, where the outer cytoplasmic foam diminishes the size of its vesicles towards its periphery, such a condition ceases to be possible; moreover the rays do not appear in divergent pairs after leaving the "attraction spheres," as, if they were due to lines of alveoli, the conditions of increasing number and decreasing size of the vesicles with increasing diameter of the egg mass would seem physically to require.

In the living egg the aster rays follow at times very waved, or truly curved, courses which are not simply complexes of lines formed by alveolar walls, but are irregular with respect to even single walls. The rays wander about also in a variety of ways as referred to above, often progressing more as filose formations than as waves of contraction influence, yet at other times gaining, or losing, emphasis in a truly contractile manner. They have no fixed course; they curve more or less from moment to moment; they extend themselves now here, now there, or conversely shorten; they even ramify and anastomose like true filose formations; yet, during such changes the surrounding, or even bordering alveoli, may show no change of contour and even no change of place.

At one point in their history they extend far beyond the median line of an as yet undivided cell mass, passing between the rays proceeding from the opposite aster, and being interlaced changefully amongst these. After an innumerable

series of changes and much wandering, they become more and more restricted in each half the mass to their own side of the plane of the coming cleavage. About this time, begins an irregular fusing of the tips of aster rays with each other, along the course of the coming plane. At first they form by this means a crooked sort of network rather parallel to the cleavage plane. This becomes more and more straightened out in its own plane, and at the same time there is a slight, but perceptible, increase of interalveolar stuff along the same plane between the alveoli, or, perhaps, merely a spreading out there of the substance of the fusing rays. At last there is a distinct pellicular, or plate-like, thickening along the coming cleavage plane.[1]

The same process being gone through with on both sides the same line, the pellicular plate is double in origin, although optically single. On each side of it for a variable time is a perfect alveolar layer of vesicles which are unlike the others of that central region of the cytoplasm, being small and like those of the general periphery; with this they are, in short, continuous in all optical appearance, being truly a preformed continuation of it. At this time the rays which spring from the "attraction sphere" are very long and in general fused at their tips with the general peripheral pellicle. At the same time similar thickenings of interalveolar substance are seen, tapering from their point of origin as they pass inwards, and ending in undifferentiated continuous substance before they reach the centrosome. This they never very closely approach since the true astral rays maintain precedence upon the alveolar structure.

Although during actual cleavage the astral rays, or certain of them, show transiently rhythmic changes which characterise true contractile fibres, I do not think that the cleavage may be assigned to this alone. For, there is a wave-like shrinking apart of the double pellicular plate, which is independent of the rays and which doubtless assists, and could accomplish it alone. It is of the same nature as the activity

[1] A somewhat similar plate-like formation was described by Carnoy for Nematode eggs, but of this I knew nothing at time of my observations.

by which the endosarc of Vorticella is split apart to form a new cleft, and represents a phenomenon common in protoplasmic masses, especially in pellicular membranes, in which one frequently sees wave-like modulations.

At different stages in their ever changing optical emphasis and physical conditions, the aster rays show that difference of reaction to chemicals which was spoken of under pellicles as characteristic of the substance in its varying states of viscidity or of contraction. A few seconds of time may make a marked difference in reaction of these structures to hardening fluids. It should also be marked that a false appearance of viscidity, or of such physical states, can be produced by too sudden changes in the density of reagents, or by osmotic conditions caused by them. There is no doubt but that methods which do large justice to finer structural relations of the protoplasmic elements, fail often to produce diagrammatic karyokinetic figures, and it is therefore peculiarly unfortunate that the presence of these structures should be made a test of preservation, or methods. On the other hand, such appearances are frequently had by less careful, more severe, or even violent processes. Besides the results of my own special experiments on this point, I have been struck with those gained by others. In one case, during efforts to improve, by re-staining, some unsatisfactory material, the investigator had plunged it by mistake from ten per cent into ninety per cent alcohol, but was rejoiced to find that it gained thereby fine karyokinetic figures of the kind sought. The astral and nuclear structures were strongly but coarsely marked and seemed destitute of all finer protoplasmic relations while the cytoplasmic structure of Bütschli was much vacuolated and altered. It seems that vitiating changes may be wrought even after an initial hardening and staining. Probably no amount of care and knowledge of the conditions to be met can be too great for such experimental research, so delicate and susceptible are the protoplasmic relations. And especially is this care needed where the irritable substance is already in a state of organized contractility.

Single fibrils in protoplasm, as well as contractile pellicles and substance membranes were seen to become waved, or tor-

tuous in line during contraction. Just so did those more complexly organized areas found in the footstalk of Vorticellidæ and in the motile appendages of all Protozoan organisms. In a similar manner were bent and made tortuous such Metazoan contractile areas as cilia, and even complex muscle bands, such as the head-attachment-muscle-band in rotifers. There seem to be conditions in which the line of more evanescent contraction waves may be held by the substance for variable periods. There are curious structural relations in the muscle of higher Metazoa which hint that this mode of obtaining more space for mass displacement has been utilised and the protoplasmic differentiation organized to increase by minute plications retractive power of the muscular machinery. Nay more, by using the added machinery of jointed endo- and exo-skeletons, such retractive plication has been still further increased ; and so the work of economic extension of energy, on the same basis always as that used for the primitive powers of the substance in its initial organizations, goes on.

[98] To sum up the foregoing: I find an enormous number of true striations and fibrillations of protoplasm over and above those optical and psychological emphases noted by Bütschli. I find, moreover, that while the latter, as lamellar films, express the arrangement and grouping or extension of alveoli; the former must be characterized as products of actual physical modification, or increment, or organization, of the continuous or interalveolar foam for physiological function. Under this head fall all the host of fibrils and filaments as well as all striations referable to filose or contractile activities of the continuous substance.

These are therefore to be regarded as substance structures, rather than as basic protoplasmic structure. They are substance tissues and substance organs.

Contractility.

[99[1]] It must be borne in mind that in discussing contraction and its allied phenomena, I speak only of those structures, or areas, or masses, of the substance in which the actual changes

[1] The whole section should be read under this number.

characteristic of contraction take place. There are always areas or masses of substance which share passively in such displacement, just as fluid alveolar inclusions do. In a Vorticella for instance, displacement of the whole body mass is caused by contraction phenomena in certain cuticular structures, aided in some cases by fibrils running through the body mass. Here the statements should be taken as referring to the active areas, not to the passive. Even in active areas there is much displacement of passive material, but this is covered by the terms of my statement.

It is to be regretted that my researches do not throw more light on the true nature of the initiative force in that mooted property of the substance, — contractility. They seem, indeed, rather to render final knowledge of this sort more difficult and improbable than it was before they were made. Whereas before, the problem rested at a certain structure which could be measured and dealt with optically to some extent, and if not referable to this, could then be handed over to the physicists for molecular hypotheses; it has now receded, — still associated it is true with the same physical structure, — but far beyond our optical resources.

Yet perhaps we are not altogether losers by these new facts, for, if, by withdrawing from our reach the elements of the problem, they seem to tend to mystification, they bring also new assurance that, so far down in the scale as substance and substance changes of this sort can be traced, or even inferred, we have still the same phenomena to deal with, and these are still associated with the same physical facts of a certain structural organization of the two sets of protoplasmic elements. By so much therefore they have more clearly defined the problem to be solved, the difficulties to be met; making ready for the touch of some master mind unified material without which the truth might hardly be grasped.

As far down as we go, we are still limited to seeing and describing the effects of contraction rather than the actual contraction phenomena. What we see is always displacement of living substance by a wave-like impulse in the direction of shortening, the displaced substance, then taking its way along

lines between the alveoli of the given vesicular structure, and in a direction at right angles to the direction of shortening.

All my facts point to but one conclusion; that as far as we can follow structure, contractility is not one simple direct change in the living substance as a mass, nor even of the continuous substance, but that in this latter too it is a complex series of phenomena, based upon the physical form of the substance as a visco-fluid foam, but nevertheless not directly explicable by these conditions.

Contraction of the living substance as visible with the highest powers is found to be always organized. This organization is always upon a basis of foam structure, either of the structure of Bütschli, or of a finer froth of the continuous elements of this. At any point it directly concerns the interalveolar substance.

Down to the limit then of microscopical vision, whatever portion of a protoplasmic mass is involved, are found those familiar phenomena which characterise muscular contraction in large masses — as of a frog's leg. That is, there is always displacement of mass at right angles to the contraction, causing increased diameter at right angles to the direction of shortening or compression. But this displacement is seen to be due, not alone to mere elastic change of shape of alveoli of Bütschli's structure, but primarily to actual displacement of interalveolar substance by a wave of contractile influence forcing it onwards along lines of least physical resistance. Whether these lines of least resistance are relaxed viscosity, or organized paths, or merely such as are afforded by the fluid foam structure cannot be definitely asserted. They pass at least between the alveoli of the existing structure along such lines as their arrangement permits. Elongation, by compression of the alveoli of the structure upon which organization of function has taken place, is due both to contraction wave and to interalveolar displacement. That the actual lamellæ of the alveoli are but passively involved in contraction, at least in its maintenance, has been shown.

These facts remind us again that, at any given moment, the true protoplasm — the living, functioning substance — is the continuous substance, and that though the inclusions and per-

haps the lamellæ of Bütschli's structure are utilised mechanically and possibly chemically also in organized contractile phenomena, they are not of prime importance.

Since the living substance wherever examined, down to the smallest subdivisions of interalveolar substance in which change of shape can be detected, showed such optical and physical phenomena as characterised contractile changes in Bütschli's structure when viewed with equally inadequate powers ; there seemed no escape from the conclusion that just so far as this must we associate with such phenomena, with such contractile manifestations of the substance as such, structural changes like those seen in gross on a basis of Bütschli's structure.

New Structural Formula for Protoplasm.

The facts as they appear to me, seem in mosaic to offer the following tentative formula for the living substance.

[100[1]] Protoplasm is a very complex emulsion, having the physical arrangement of a very finely subdivided, variably viscid, foam, which characters are coextensive with the continuous element of all visible optical reticula.

The substance which at any given moment forms in all subdivisions of the foam the continuous element, varies its viscidity by some unexplained changes within its finer structure, so that from a very fluid state it may almost instantly become viscid to varying degrees, even to a semblance of true solidity. It is subject to displacement by contraction activity which may be rhythmically organized, or may be of a filose nature. Such changes may affect all, or a part only, of visible reticula, so as to form of the interalveolar substance simple or compound fibrils, or threads, or plates, of a different physical and optical quality. These having necessarily the course of the continuous substance must form optical striæ simple or branched, or an optical reticulum, the arrangement of whose lines, but not whose mass, is governed by mode of distribution of the emulsive inclusions.

The continuous substance is at any given moment the physi-

[1] The whole section should be read under the head of this bracketed number.

ologically active element of protoplasmic masses. In its last resolvable arrangement it has always the form of a pellicle or membrane surrounding fluid inclusions. It is the contractile and irritable substance. It forms all living contact surfaces. It is the sentient substance.[1] It is the bearer of those physiological powers, functions, habits, and instincts which characterise the living substance. Upon its response in character of its powers, or properties, to specific and general environment, depend all the physiological phenomena characterising areas, masses, or organisms, as such. It is homogeneous throughout all areas alike, as to its intrinsic powers and characters, but not as to the specific, or habitual, expression of these, which varies with its chemical or physical contacts. (See following sections.)

All pathological or abnormal states of the organism, or of organs or areas, are directly due to abnormal states of the continuous substance, and secondarily to abnormal difference in the specific or immediate stimuli for this; either in the affected area or in those which control, or are controlled by, it. Death of the organism or the area is due to irretrievable disorganization of the continuous substance in the chief tributary areas or in the whole area. The initial stages of decomposition are always the dissolution of an organized arrangement of the continuous substance, and, after variable protoplastic activities of this, a dissolution of its organized finer structure, and the replacing of both organizations by a purely physical vesiculation having an optical appearance of a fine structure of Bütschli.[2]

The discontinuous elements, or protoplasmic inclusions, are most heterogeneous, in their ultimate subdivisions defying chemical analysis, as they do all effort to separate them optically from the lamellæ of the continuous element as such.

They form the chemical contacts or specific controls, that is, *the specific environment*, of the living substance. They are the secretions, assimilation products, excretions, and hoarded reserves of the living substance proper. In Bütschli's structure

[1] See following sections.

[2] This statement is the outcome of many direct experiments with areas of living organisms and whole organisms.

they seem in general to play a passive mechanical or physical rôle and are strongly hinted by the phenomena to be for the most part, and for most times, segregated excess, waste, or reserve material of the living substance.

By holding the place of continuous element in the protoplasmic foam, the living substance has its contact, or more strictly speaking, its contacts, almost infinitely extended and multiplied. For every pellicle is a contact surface of the irritable substance as such, and a possible contractile membrane; and to this every alveolar inclusion, as well as every local difference or activity within actual touch of it, bears as truly a relation of stimulus or control, as does external environment to the substance as organism.

To the irritable substance, contact is stimulus: to the living substance, contact is environment.

Heretofore in biology, environment has been used in rather a limited sense for the sum of influences which affect an organism from without, as opposed to its own intrinsic forces; therefore as modifier of its inherent tendencies as organism, and chief factor in determining the final result of organization.

From the new standpoint of the substance as such, which it is my privilege to preach, biological use of the term environment must be widened to give it its full value carrying our thought of it into the minutest subdivisions of living substance.

It is at once plain what a magnificent device is the physical form of the substance for multiplying and extending contacts; and, given the physical variant of viscidity, as well for preserving, conserving, and unifying, stimuli; for segregating inconvenient and inutile substances; and for providing at any point a homogeneous basis for organized activities. As by convolutions in the brain, thought surface has been, and may yet be, greatly extended; so by structural subdivisions of a fluid foam, the environment of the living substance can be extended and multiplied until it may even be coextensive with a primal irritable stuff.

For what is at first but a minute and momentary contact for the substance as mass or organism, can presently be transformed into contact for the substance as such, which is now limited

optically by subdivisions of a visible structure, but which the known subdivisions of this again extend, and which the phenomena of the invisible substance prove to have no limit assignable by us. A concrete instance will help to an understanding of this broad statement.

When an amœba, responsive to the touch of a passing organism, engulfs it, the protoplasm, obedient to its physical form, surrounds as a pellicle the ingested mass, and thus that first slight point of external touch becomes at once extended into an internal contact many hundred, or thousand, times its first area. As digestion proceeds, the chemically altered food becomes more or less a watery solution and in this form is gradually diffused throughout the whole organism until, both by this and by wandering of interalveolar material and of vesicles of Bütschli's structure, the living substance may to its farthest morsel suffer change of environment, which may be by way of extension, or renovation, or actual change, of stimuli at multiple contact surfaces formed by lamellar films.

Thus by ingestion of food is the specific environment of the substance not only extended but perennially renewed. Nor do the phenomena differ in any essential in those higher organisms furnished with most stable and complex machinery for the distribution as well as ingestion of food. These facts hint that there is a more extended significance than has been understood in the habit of reducing food substances to a diffusible form, for they are now seen to be thus prepared not for the stomach membrane only, but for the universal physical form of the living substance.

The subdivisibility of the foam structure, the general physical plasticity of such a form, plays an important rôle in arrangement, and in procuration also, of specific, internal environments for the living contact surfaces or vesicular films. For, as was shown above, relatively large quantities of inclusion substances, as well as of living substance, can be transported through, or amongst, very stably organized areas of physiological function to other parts of the mass, or even outside it.

From the physical form of the substance results great economy too of the vital stuff. Growth of areas, masses, or

organisms can be effected to an enormous degree by mere accretion of passive, non-living material, without the actual living stuff being increased at all, for there is a very wide range to the thinness of alveolar films in each structural series. The amount of true living material, as we know it even, is probably very small in any organism. In the young organism, notably in the developing egg, the network substance is often markedly thicker than it is in later stages. In the minnow's egg and in the starfish egg this was beautifully shown. While this may not be a rule it is true of many cases. Again, one adult organism may be larger than another and still hold actually much less of the living substance.

From the physical form of the substance, again, arises infinite opportunity for contractile service of an organized sort. Of physical necessity, the very contact between two vesicles produces planes and lines of continuous and direct field for organized contractility, — nay almost compels it, if the irritable and contractile nature of the lamellar substance be taken into account.

For receiving and transmitting physically all physical impacts, as well as for appropriating or reacting to, chemical contacts, it would be difficult to conceive of any combination more perfect than that afforded by the multiplied and extended lamellar membranes of widely variable viscosity and tenuity and curvature which the facts have seemed to express as the form of the living, irritable, contractile, sentient, substance.

The Living Substance; as Such; and as Organism.

As indicated in areal differentiation, the problems confronting us in organization of the foam elements in their specific relation to each other, are but those with which we must deal in understanding the origin of physiological organs or areas, not excepting those of the highest organisms.

[101] Conversely, it is even more true that the problems confronting us in the most complex and stable organs of the higher animals are identical with the problems found in the living substance as such, to its smallest visible subdivisions. Nor does it end here, for there is indubitable evidence of

protoplasmic extensions invisible to our strongest magnification, having still the same structure, the same characteristic displacements, which would yield to bettered tools the same optical phenomena as belong to large organized masses,— such, in short, as pertain to the characteristic physiological activities of protoplasm.

[102] Bütschli found that mass has much to do with the relative character and duration of phenomena in his artificial foams. The living substance seems to transcend such physical limitations. That these statements are not merely wild speculation or inference may be shown anew by a single instance, and it is thought that the filose phenomena cited previously also bear them out. Many others could be brought in evidence but for lack of space.

The cup-shaped film, or "collar" of many Choano-Flagellata is so tenuous in greatest extension that when magnified eight thousand diameters, though it may be visible obliquely and laterally, one cannot see it in direct, transverse, optical extension, not even as a hair line; yet it is even then thicker than many webs and veils Gromia extends.

By addition of pigment to the water a double set of currents can be demonstrated in this film. One current flows up and out from the body over the outside of the collar to its edge. Turning this, it then flows down the inside, back towards the body substance with which it mingles. Small organisms brought against the outside of the collar by rotary beat of the single projecting flagellum that springs centrally from the anterior end of the body, are carried along to the body substance which engulfs them in usual protoplast fashion.[1] At times the collar assumes considerable rigidity and the flow ceases for many moments. I find that if a jar be given the cover glass, the fluid, flowing film instantly contracts, taking the form of a truncated cone. During this contraction, striæ appear which run from the top downwards, gradually thinning, fanning out, and fading away as they near the base of the cone. Conversely, they are

[1] These phenomena were first described by Saville Kent whose faithful, patient researches among minute organisms have yet to receive their full meed of appreciation from biologists. In my own researches I have ever found Kent's work preëminently accurate and fine.

more marked and refractive as they near the edge, where they are so closely set together as to appear fused into a thick, highly refractive rim. At this time the collar has perceptible and constant viscidity, amounting to rigidity, for it bends not at all to sharp pressure from other larger organisms, as from the appendages of Stylonichia moving about it.

From the standpoint of a physical and mechanical hypothesis, what marvellous and irrevocable transformations of substance must instantaneously have taken place in response to that passing jar of the cover glass!

Yet after a few moments' quiet the striæ begin to be less distinct and the shape of the collar shows a new change. It opens now at the top, widening gradually until it again equals its first expansion. As it nears this limit, another set of striæ, but far more delicate, appears encircling the collar, that is, transversely to the first set which has by then quite disappeared. Finally all striation vanishes, and by their renewed movement up and down over the surface of the film the pigment granules show that the former fluid state is again active. That it is truly a fluid state is shown by the whole film being at other moments returned by flow into the body and then again extruded in any one of a number of fantastic ways. It may appear next as an amœboid mass extending lobose processes, or beyond these filose threads, or as a huge bubble of protoplasm such as Vorticellidæ are found blowing, the walls of which may here be thick or thin, smooth or variably lumpy. This will thin out more and more at the uppermost convexity until it seems to burst like a bubble. After this the whole expands itself gradually, — the irregular protoplasm returning into the body, — and the normal appearance of the "collar" is restored. The flagellum may be reproduced from the centre of the collar included area by an irregular pseudopodial process which undergoes swift reconstruction until the normal flagellum is again actively functioning.

The collar will again later suffer metamorphosis into some new mask for the substance. How unimportant here does the form of the substance seem in comparison with its habit!

If a cross section of a collar film could be made, equalling in depth the thickness of the film, we should have a filose-like

mass, invisible except when in a contracted state, yet wide enough for a double set of substance currents to flow upon each other, and possibly with even a third supporting area between them, such as obtains in many filose extensions of protoplasm; wide enough it certainly proves itself to contain the substance and much structure, and room enough for such structural organizations and changes as are associated with intermittent organized contraction. From the outer surface of the cup were sent off at times delicate filose processes whose mass being great compared with that of the film looked quite large. These have been taken by some observers to be adherent bacteria.

[103] In Gromia the contraction phenomena of threads and webs are even more marvellous. Such facts, with others previously cited for filose activities, go far to convince one that to limit protoplasm and protoplasmic phenomena and protoplasmic physiological structure to those grosser masses we now discern would be to stultify ourselves and to lose many chances for valuable effort. If Biology is to be the guide of physiological, medical, and hygienic science, which would seem to be her highest function, it is such minutiæ of life history and possibilities of the living substance, which offer best fruit to that willing patience, that single-hearted, loving receptiveness of research for which human progress ever waits and upon which it still must lean.

One cannot but wonder with a child-like wonder, at the infinite smallness possible to the living substance as such, and even as organism, but to refuse credence because of this unimaginableness would be as childish as for one who had never looked through a microscope to disbelieve in the Protozoa altogether; as childish as to refuse to believe in those hosts of mighty stars which for the naked eye have no being.

The nature of a physical foam such as postulated here, makes possible for protoplasm a disposition of its elements in such minute sub-divisions as water has in air; makes it possible for the substance as such when seen from afar, — as with our poor optical powers we still must see it, — to look as still and structureless as those cloud masses which seem to hang motionless

for long days upon a mountain peak, but which when climbed to and met in close encounter, are found to be hurtling masses of vapour, rushing powerfully against the crag on one side and melting away like an elusive memory as they strike a wall of warm air just beyond, while every foot, every inch, of those square miles of vapour is stir and changeful difference.

[104] The marvels of filose phenomena have been dwelt on at length. It is not undue emphasis has been given them for they are by far the most widespread and most characteristic phenomena of the substance, if we except contractility.

In ordinary amœboid movement there are two sets of phenomena to be reckoned with; a purely passive flow governed by impetus received from local substance contractions; and a more mingled flow in which the same cause lasts longer and passes as a wave of contraction along certain lines of the substance causing more or less steady and continuous displacement before it of the substance in its path—like that of interalveolar substance along the fibrils, or as in filose phenomena.[1]

In amœboid displays the structure of Bütschli or a coarser is largely implicated, the finer foam of the continuous substance being of course involved. In true filose activities the displacement is limited to the finer froth. This expresses I think, the whole ground of difference between them. I do not deny to protoplasm motion of the sort which Bütschli

[1] Having spent hundreds of hours in watching the flow of amœbæ as well as of many other and diverse Protoplasta both lobose and filose, besides Myxomycetes; I venture thus to express myself counter to certain widely accepted opinions. The phenomena have been looked at too much from a standpoint which accepts the most obvious phenomena as of prime importance, using these for the starting point of observation; and which is further baffled by that most treacherous of all relations, a time, or sequence, relation, arguing *post hoc ergo propter hoc*. The subtlety, complexity, and fleetingness, of protoplastic phenomena at their simplest, together with the fact that at any given moment many causes and many effects are crossing each other as impulses and impulsions of fluid and readily displaced substance; have seemed to me to make the study of amœboid phenomena quite other than one could imagine from any printed description to be met with. One might easily give a lifetime to unravelling these phenomena and without much result if one followed the established precedent in this line, that is, looking for and seizing upon change of external contour, and grosser internal and external displacements and correlating these which, as a matter of fact, apart from mere mechanical displacement caused at times by impetus of one or another, have usually little or no vital relation to each other.

demonstrated in his physical foams, for these researches proved nothing for me more conclusively than that the physical opportunities of its form are made large use of by the living substance. But this is mere incident in its whole life history.

[105] All the facts relating to the filose habit of the substance are most interesting when taken in relation to the possibility that Metazoa had their rise not from an ancestral amœboid stem but from an ancestral rhizome of Filosa. The new facts seem to suggest that the Metazoa arose rather from a filose type which by coalescence, or areal differentiation, built itself up into compound masses. If by coalescence, the substance as such showed respect to that position in the mass in which it newly found itself, exactly as in each individual it had through all its ceaseless flux respected its relative position; for it must not be forgotten that in these protoplasts the substance as such is ever changing its position in the mass or organism.

By such hypothesis, complexity of organisms would arise by extension and multiplication of areal differentiations which were but rearrangements and redistributions of the two sets of foam elements in relation to each other; in short by mere continuance and extension of exactly the same state of things that existed in the individual as a starting point.

This hypothesis would be a true description of the phenomena which can be seen to take place in development of a starfish, sea-urchin, rotifer, annelid, frog, or hen's egg.

It is a very difficult thing to grasp this idea of a sensitiveness of the substance as such to its position in the mass; it certainly would not occur to one *à priori*. The reader is reminded of the viscosity rhythms of the substance in sea-urchin and starfish as correlated with its position in the whole mass whether this were of single cells or of many cells. In all protoplasts the same thing is seen. In the phenomena of leucocytes of crab's blood it seems that organization of this sort is instinctive among even wandering cells of a Metazoan organism, under even novel stimulus of opportunity or external conditions.

A still clearer understanding of what is here meant can be given by citation of an organism which, before the heart of these researches was reached, was thought to be from the cell

standpoint a missing link between Protozoa and Metazoa. From the standpoint formulated by my facts, from the standpoint of the substance, it is now seen to be even more valuable as a link between these two, and as a most expressive type of substance life writ larger than common.

There is a Heliozoan described by Leidy and others, *Raphidiophrys elegans*, which lives at times as isolated individuals, and then again, for variably long or short periods, in coalescence with others to form a wandering colony.

As single individuals, the animal does not differ from all typical Heliozoa. Its filose pseudopodia are used for locomotion, for prehension of food, for tactile purposes, — for what else we simply do not know. In its isolated state, these processes are freely produced on all sides of the periphery, and are on all sides alike in kind as in origin and function.

In the coalesced, or compound, state, the individuals form a colony whose units are separated from, as they are joined to, each other by bands or bridge-like extensions of protoplasm which are formed by modification of the usual processes and make living links between the animals. Between these bands the water surrounds the colony everywhere.

The remarkable thing is that no matter what may be the number of individuals so coalesced, and Leidy states colonies contain at times upwards of thirty (I have not seen so many), the usual filose pseudopodia are formed only at the periphery of the whole mass. That is, each *Raphidiophrys* lays aside, for the term of its union with the others, the habit of filose formation at all those portions of its mass, which, though peripheral still to itself, are not peripheral to the colony as such. From those portions of each unit, which, through coalescence, become in a sense interior to the colonial mass, there are produced only bands or bridges of thick protoplasm, both ectosarc and endosarc in their usual relations to each other, and these form the ties between the individuals. Those units which are wholly internal to the colonial mass, produce no filose processes but only connecting bands.

Two points of utmost weight must be given due emphasis in studying this physiological marvel. First, that the substance

of each individual is in ceaseless change of position with respect to the mass of that unit; and further, with respect to the mass of the colonial organism as such; besides which, there is the ceaseless interchange of substance and function between ectosarc and endosarc, and finally a ceaseless interchange of substance between the units. The units are covered throughout, over their whole periphery, by the usual ectosarcal formation.

[106] For the substance as such, then, there is no quiet nor any persistence of position. Yet each portion of that substance, wherever it passes or pauses, knows where it is and how to play its part as citizen-substance of the coalition. Surely this is more marvellous than the imagined stable diversity and interaction of Metazoan cells, if indeed we still dare to say that in them is greater actual repose of the substance as such beneath the mask of form of organ and organism.

The final touch to wonder is given when it is seen that the units of this coalition are, as organisms, surrounded at all points exactly as usual by their normal external environment, for at first they are joined by their filose processes between and around which, as later with respect to the bands, the water freely passes.

If, in the starfish egg, the phenomena are such as to incline one, if one does not bow to the mosaic hypothesis, to think there must be in the egg some coördinating area or factor which it, as organism, possesses, — a sort of brain direction owned by all the cells in common, — how can one bring such an interpretation into play here, where the units are not parts of a single mass formed at one time by one parent, nor even indirect products of two which peculiarly dovetail their properties and "ids"; but is a coalition of stranger organisms. In which should one say the control resides? Or shall we think one unit perhaps assumes entire direction while the rest hold in abeyance their control power as they hold part of their pseudopodial formation? Then how is this common harmony of action got at? And how reconcile it with the retention in part of control by the units? For it is hard, too hard indeed for me, to believe that the single controlling centre would be able to manage this feat. Finally, how can the units as such

be in any case under such control from one centre when the substance of the whole is in ceaseless flux from one to the other of the whole group and in all parts of the units.

[107] The control in this case must, it seems to me, *be intrinsic to the substance as such, and not to the substance as organism.* I think, in short, that one must reasonably believe that the living substance, as far as it can be traced optically, is not only irritable and contractile substance, *but that it is already conscious organism.* By conscious I mean that more basic form of it which I have above termed sentience. And I think that the phenomena recited already in this paper will of themselves alone bear out to great extent such a conclusion. Sentient, but subject to such direction from organized centres of this same sentience as may be supplied by the nucleus, and other areas of organized differentiation, as the cytoplasmic granules, — I assert the living substance to be.

The complacency with which the facts on all sides of my investigations lend themselves to a founding of the Metazoa on an ancestral rhizome of Filosa, is reflected in these further characteristics of the Filosa. The Filosa, as I should widen the use of that term, are by far the most numerous and widely distributed so far as we know, for they would include all marine Heliozoa, and the Radiolaria as well as the Foraminifera, including Gromia and similar forms. As a group they are marked by a tendency to coalesce; and to multiply the nuclei without actual separation of nucleated areas. As a group they are marked by a plasticity of organization, and show a tendency to areal differentiation of structure and a power of adaptation to general environmental conditions in a number of ways, notably by formation of free-swimming, flagellate, larval, masses. Their differentiation is of the special character which I find to distinguish animal organization; that is, it tends to emphasis and intensification of irritable and contractile function by organization of the elements upon an ectosarcal basis.

As a class the Filosa are marked by habits of substance metamorphosis for purposes of perpetuation, such as formation of free-swimming, flagellate larvæ, and also of a minute germ-like posterity which are freely motile and suggest sperm.

Besides this, they bud, and multiply by fission also in many cases.

As a class they have a habit of, or tendency to, actually conjugate, which must not be confused with the mere coalition phenomena, for in this former case the nuclei of the individuals, which may be two or more, are diffused for the time and then again reorganized. These actions result after variable periods, it has been observed, in reproductive phenomena, and so the Filosa are open to the increased plasticity of destiny which such a mingling of individual masses or substance seems to produce in the substance within fixed limits.

[108] To sum up the above remarks, my mind is drawn with some force by the suitability in all ways of the filose protoplasts, in habit as well as in form, for the evolution of a race of compound and complexly differentiated substance masses, with multiplied latent possibilities, all parts of which seem to retain to greater or less extent the spinning habit.

True Biological Standpoint.

[109] But after all, whether we consider past forms as the root of present forms, or these by themselves, the thing of greatest moment to us is neither form nor structure in linked gradation from age to age, but rather that of which all form, all structure, are but the casting, the mould, the framework, and the mask. It is the living substance as such, its fleeting activities and their meaning which should concern us most.

[110] Surely all the facts urge a somewhat changed standpoint in biological research. We are not denied an ultimate return to purely physical interpretations. These are not yet pronounced impossible nor even improbable; but we are bidden for the time to a physiological standpoint as more immediately fruitful. That there is a physical machine seems now more than ever certain, but that the machine within our present ken is the wonder-working machine, seems less than ever predicable. We are forced to see that the final automaton, if such there be, must be allowed to be, within an incredibly minute mass, almost infinitely self adaptive to innumerable contingencies.

The final problem falls thus, for the time, wholly within the realm of metaphysics, and the biologist must become again the naturalist if he is to win from his toil anything but negative results.

[111] The facts seem to me to instruct us that, to the living substance as such, form, as well as size, is mere incident. Structure, so far as it has been detected or inferred, becomes for the time being secondary in importance, as it is in origin, to the habit of the substance; and we are warned that when regard is had chiefly to visible structure as such, or when this is taken to be an explanation of phenomena rather than an expression of substance habit; when it is taken tq be the cause rather than the effect; the record becomes to us a cypher instead of language.

[112] For structure, as far as I have traced it, was still seen to be a mask behind which the most important business of the living world is carried on undetected.

Nature might well be likened to a great spider, spinning and spinning the living stuff and weaving it into tapestries; and still hiding herself and the ever-lengthening thread of vital phenomena behind the web already spun. To nature, the fact of prime importance seems to be the substance,— the substance —the substance; whether as mass, area, organ, or organism. Nothing seems to be of great account with her compared with the character and possibilities of the material she is dealing with, — and truly it is a most plastic stuff.

One realises in thinking over such facts as have been here described, that, from this standpoint, man's classifications, though significant, are not inviolable. He has concerned himself chiefly with individuals, organisms, species, and races; with form, and with structure as the exponent of form.

But it is to the living substance as such that all nature's pliant cherishing has regard. Form and structure are used to this end; they are not in themselves ends for her. From such a standpoint, distinction between individual organisms and the substance as such is mere child's play. That has been man's game with the substance which he has found strewn about him in pieces he can grasp, arrange in lines and group as he will; —

as a child might arrange the pieces of a puzzle whose total significance is beyond him; wondering to find upon so many isolated pieces the same bright colours; trying by these to make connection, but little dreaming that the whole is built up on a system of grand but subtle lines to which the colour, although limited here and there by them, is mere incident.

From this standpoint, animals, even man the animal's lord, is but a piece of the sacred substance, mingled with an enormous proportion of alien and valueless material. It is nothing to nature then what happens to this or that individual, species family, or race even. Before these fall like a leaf from their place, some most precious substance has already been massed under her guidance in other storehouses, or is on its way to yet more secure keeping; or the triumphant substance in other forms proved better fitted to the new conditions. Again and again the facts repeat that form is little or nothing except as a means to this end. Whatever form will best preserve the living stuff, whatever modifications it can best be cherished by, are seized on. As conditions change, one disguise after another is assumed by the substance as such that it may run the gauntlet of adverse, or hostile, conditions.

Transmigration is thus seen to be a strictly biological truth. In this, too, is rooted nature's apparent cruelty. Creatures destroy each other, but nothing is lost; the substance is rather actually strengthened. Barring the outcome for the substance as such, it is all one to nature whether the bacterium or the Buddha win.[1] The living substance is free to determine its own fate, so only that that substance, stronger and subtler and more powerful to control its own immediate conditions survive. It is as though the multiplication of forms and individuals were but a device by means of which the substance as such should be strengthened, — as though a man were to practise one hand against the other to increase the strength of either.[2] The individual is part of the game, and the conscious or semi-conscious

[1] The ideas of nature and of a deity are not to be confused here, for "God is a Spirit" and something, I conceive, quite apart from the order of physiological nature as dealt with here.

[2] I use device always in the sense in which a mechanician uses it.

antagonism of the individual to that truth is merely a useful factor in the fact. (See Fosterhood and Heredity.)

[113] Degeneration, or simplification of form and structure, are often as useful to the substance as increased complexity or emphasis of function. Its business is to use or to evade its environmental conditions. Nature busies herself ceaselessly with and for the living substance as such. Transplanting, grafting, pruning, and fostering she still keeps it fresh, young and unwearied. The separation of one portion of it from another in those masses which we call individuals means something quite different to her. To her the living substance is everywhere continuous. The strange, inseparable, duplex or triplex relation of parent and offspring substance is but a single though strong hint of her attitude in this respect. (See Fosterhood.)

[114] Only when the biologist knows his substance directly in living states can he learn it argumentatively from preserved material in cases where the living states are perforce hidden from him. He must choose to know it as a living substance rather than as dead coral reefs of structure. *He must study it as activity rather than as product; — as a ceaseless becoming, rather than as an achieved and rigid fact.* Chief of all that these researches hope to accomplish is to tempt the biologist from the artificial, the dogmatic, the systematic, mode of study; to tempt him to observe the living substance in its haunts of structure, in the same way that a naturalist watches the habit of the organism as such; to tempt him to a pursuit of substance life, substance structure, and above all substance habit. These he will surely find so absorbing that his microtome and paraffine bath will rust to uselessness on his shelf before he next turns to take them down, — after such patient devotion of seeing what is to be seen without them, that he will to some extent know what he is looking for by their aid.

If the biologist, in such a naturalist-like pursuit of the phenomena of the substance will cultivate the naïve rather than the learned standpoint; if he will isolate and perfect so far as possible his animal faculties and perceptions, such as wild animals

use in their daily life, and such as conjurors make use of in their sleight of hand and second-sight tricks; he will gain for some time to come more knowledge of the living substance as such than if he applied the whole weight of historical and conceptive training to bear on the difficulties. There is to be seen amongst expert manual labour and the expert knowledge gained in the mercantile business of the world, a far higher and more delicate cultivation of the perceptions necessary for just this work than is to be found among scientific men who have spent years in so-called laboratory training.

If after his perfecting, so far as possible, these animal faculties the biologist finds himself seemingly as far as ever from the goal of perfect grasp of the ways and expressions of the living substance as such; he has only to recall how difficult it is for him to follow the gross movements of whole and large organisms across large spaces, — the utter baffling of his keenest attention which is possible to human hands, arms, or even a whole body. Thus he will regain a large patience with his defeat and be content to serve seven years to learn more of the movements and habits of the living substance as such. He will then learn how strong, how yielding; how bond, how free; that substance is; how seemingly wayward, and yet to the limit of our opportunities of knowing it, an expression of disciplined and unified results, sympathetic to the sum of past experiences, — prophetic of the sum of life yet unlived.

[115] To concern oneself much with the living substance as such; with the habit of the substance, rather than its form; to see, to understand, how the substance expresses itself in relation to its environment, both general and specific; to follow it in its complex action and reaction; to learn how it uses, rejects, transcends, or passively protects itself against external conditions; and how it bends itself before these in order to conquer by a magnificent "jiujutsu": this seems to me the true biological standpoint, for it is the standpoint of the living substance as such, — it is the working standpoint of nature.

SELECTION OF ENVIRONMENT BY THE LIVING SUBSTANCE.

I have shown that throughout the Metazoan mass, as throughout the Protozoan, physiological function is correlated with areal organization of the elements of the emulsive foam. In the former as in the latter, organs are areas of vesicular organization; and in either, all such areas however fleeting are true substance organs.

In the higher forms, there is a more fixed and definite habit of structural arrangement, certain relative localities being fixed for grouping certain discontinuous elements in a certain way; while in the lower forms, locality for any given mode of organization may be as unstable within certain limits as the substance itself.

[116] Nothing new by way of minute structure visible with the microscope was seen in the most complex of the series of organisms examined; but merely a more extended and multiple and stable organization of the foam elements, and of the habit of the substance in correlation with these things; the contact relations thus brought about resulting in quantitative and qualitative emphasis of physiological function, and a more extended control by the substance as organism of its general environment as a source of supply, or control of its own use of supplies obtained from that source.

[117] We are so used to limit our notions of environment of living beings to the external world, and to ignore that which forms for the substance a large internal world of contacts and opportunities; so used to think of environment as in a way dissociated from — nay, even antithetical to — organisms, that it may be difficult, perhaps, to think all at once of external environment as a mass of heterogeneous conditions bearing to the external contact surface of organisms the same relation that the blood of a frog, for instance, or the contents of a food sac of amœba, or even of an alveolus of a structure of Bütschli, bears to the substance surrounding it. The ancient warfare of the race with environment hinders us, indeed, in grasping the truth of these relations and realizing that external environment is to the substance as organism akin to the sum of internal environment for the substance as such.

Living organisms are surrounded as masses by a general external pellicle of protoplasmic membrane, within and continuous with which, is a complex web of delicate, irritable, contractile, membranes. The mass pellicle, whether it define the limit of one or of innumerable cells, expresses the contact surface of the organism as such in its relation with environment. For it, environment is of a twofold nature, being compounded of an internal and an external set of contact conditions.

The external set of conditions is, to great degree, beyond control of the substance, except indirectly through aid of its internal environment which bears a constant relation in both kind and arrangement to the needs of the physiological powers of the substance, and seems to be controlled by it in a twofold way.

The internal web of protoplasm, on the other hand, is physically surrounded by, and in contact with, an environment upon which it acts and to which it reacts in a multiplicity of ways. This is more or less completely within its control, yet influences it largely and even to some extent controls it; physically and chemically. Being met here by the undying question of priority of control, it is possible to say only, that, granting a possibly complete, final control of the substance by physical and chemical conditions, yet in the existing state of things visible to us as structure, the substance is seen acting through and upon an existing internal environment. In this way the certain conditions necessary for its renewal are detected, pursued and chosen by the organism. These the living substance as such, acting still through existing internal conditions, proceeds to transmute and to arrange with reference to its own general and local needs.

[118] The internal environment of the living substance is finally, as has been shown, inseparable for us from lamellar subdivisions of the interalveolar foam. Even supposing we could isolate and retain in a living condition for this purpose considerable quantities of the continuous substance of Bütschli's structure, it would be impossible by the most minute chemical analysis to determine more of even constant results — such as proteids — than that they were either necessary constitu-

ents of the living substance; or constant products of its activities; or a necessary and invariable part of its most intimate conditioning.[1] And whatever may be the destiny of the materials introduced into, or formed by chemical activities within, the living substance, their first, inescapable, function is assuredly as pellicular or lamellar environment.

Such physical and chemical conditions as are introduced into protoplasm yield but heterogeneous stimuli — a most mixed environment — for the substance. Since for organized activity, organized specific environment, is needed and provided, the bringing together, the chemical preparation, and the peculiar grouping, of the various substances which serve in this capacity, form the problem to be solved.

[119] In non-living, or perfectly inert foams, there is a tendency for vesicles of similar size and bearing similar contents to become gradually grouped together, and for these latter where fluid to coalesce. It is not such mechanical aggregations as these we must explain in protoplasm, but such aggregations and such segregations as take place under conditions seeming to contradict those demanded by the given physical explanation. We must account often for a subdivision or reduction in size of these kindred inclusions when brought together, and for specific redistributions of the continuous substance: We must explain complex deportations of substances from areas where physiological activities of a sort to which these are physically an impediment appear later; and, in other areas, a rapid massing together of inclusions peculiarly favourable or necessary to the physiological functions called for there. Most difficult of all, we must account for these physically complex and highly organized phenomena taking place almost instantaneously as response, not only to specific chemical or physical environment of an accustomed sort, but to a wide range of such stimuli, even those never before experienced, and to very local stimuli, of a purely physical nature applied to some distant area of the organism; the physiological response being often made in defiance of certain strong physical handicaps in environmental conditions.

[1] Finding none suitable, I am forced to create this noun for a term of my results.

[120] Though finally inexplicable, the phenomena may be formulated in a way which at least unifies the difficulties and places the problem in a form more easily grasped and handled, when it, like all the radical questions already presented, is seen to be a question that pertains to the substance as such. Like them, it is but writ large in the organism; like them, it may also be tracked to the ultimate visible subdivisions of the substance and found to exist there unchanged in its nature. It may be called ***the selective power of the living substance with regard to its own environment, both general and specific.***

Turn where we will in the kingdom of living things, the substance in all its complex phenomena, in all its manifold forms and phases is still seen to be in act of either pursuing, securing, disposing of, transmuting, or using as stimuli, its peculiar internal environmental conditions, — the latter phenomena being but varied aspects of the former. From the amœba to man, it is certain that the substance as organism selects from the sum total of environmental opportunities what it needs for its own specific internal environment, that is, the environment for the substance as such in all its subdivisions.

The most obvious form of this selection is seen in ingestion. The cow eats plants, the tiger eats flesh, man eats both flesh and plants and a thousand things besides, the creation of his fancy; — but all eat as living substance seeking its own environment, for these acts of the substance as organism are followed by kindred activities of the substance as such throughout its most minute extensions, the inter- and intra-alveolar filose activities being doubtless instrumental in attaining these ends, — and osmosis as a means is largely provided for by the physical form of the substance. (See above, New Structural Formula.)

[121] From a heterogeneous environment, common to all, each substance self takes, then, what will preserve, or create, for it its own special, internal, environmental conditions. Where the initial selection is made broadly, roughly, with seeming carelessness, or even wrongly by the substance as organism, the substance as such makes choice again within its safe precincts, and again within its more secret haunts where we can

presently no longer follow it, extending and repeating the selection until all the protoplasm has chosen for itself, or passed by, or rejected, for itself, and secured, so far as the opportunities allowed, those special environmental conditions by which its general and its specific activities may be maintained.

Later, when all the ingested matter has been passed upon thus, the substance as organism finally rejects and casts out all the leavings of the substance as such, together with such waste materials as have been thrown off by this during function. In addition to direct methods of ejection, there are many indirect methods and also many special substance devices for getting rid by more roundabout ways of deleterious, or cumbersome, or inutile, matter. Area after area of organized physiological difference may be incited by presence of ingested food, to produce such secretions as will aid in preparing it for that diffusible state in which it can reach and be used as opportunities by the ultimate lamellar subdivisions of continuous substance in all parts of the organism. These areas are indirectly incited, not by actual contact with the food, and they act through their own existing conditions to aid in preparing what may later furnish renewal of their own powers.

[122] Actively by means of its physiological powers, and passively by its chemical and physical nature and properties, the substance secures a double series of judgments on its internal environment. Then by new combinations and devices of areal differentiation, always on the basis of the foam structure, it constantly extends its power of dealing as living substance with the heterogeneous opportunities of environment.

[123] To restate; in securing its own environment, the substance, both as such and as organism, exercises among the sum of opportunities offered it by external environment — a choice; and in this choice manifests its own character. The words "choice" and "selection" need carry no implication of conscious action on the part of the selecting substance. They may be understood without further weight than is given the selection by a magnet of some steel filings from amongst glass and sawdust particles; or a choice by the steel filings of

the magnet rather than of the fingers that hold it; or even despotic chemical and physical interactions. A taking of one sort of thing from a number of associated and mingled opportunities, — this is all the physicist or chemist biologist need suppose is claimed at this point.

At times, the substance as organism selects or accepts materials which some specialized sentinel area within it refuses to pass, compelling an organism to reject them secondarily. There are certain areas which seem to be detailed to serve the organism thus and to pass for universal needs of the substance as such upon material admitted within it. In this connection the instance cited of expulsion of bacteria by a Vorticella, and of regurgitation by rotifers of their food, may again be brought into play. Every one knows the drastic action taken at times by different areas of the human body with respect to wrong sorts of internal environment. The most curious of substance devices to rid itself of undesirable internal conditions, is found in scavenger areas — leucocytes and phagocytes — which are so individualized that they select for their own specific environment what is deleterious to the substance in general. They are also used to take up surplus material of various sorts which interferes with normal activities of areas or the organism. Their function is doubtless homologized for the substance as such by migrant currents and filose processes of the interalveolar stuff.

That the organism makes even fatal mistakes at times in choice of its environment is true, but this is generally caused by lack of perfect subordination of the function of areas to the needs of the organism as such, for these by their very emphasis of irritable function may be led, for their own satisfaction, to wrong the rest of the mass; or there may be inescapable physical and chemical affinities which decide the matter, and the organism be taken by surprise; or there may be an abnormal state in the purveyor area. Deleterious substances that have gone too far to be returned are often hurried through the organism, or surrounded by some corrective or insulating substance which prevents their doing harm; or again, if harm be inescapable, the powers of the substance are

seen in a new phase, for peculiarly suitable unusual secretions are poured forth as antidotal or cleansing agents. Local efforts of the substance to expel or escape or counteract injurious materials can cause disease or even death of the organism, which then must be counted an indirect and not a direct result of the inimical agents.

With regard to a taking up by living cells of useless or even harmful substances, especially during artificial experiment, certain things are to be thought of. First, that the conditionings of the living substance must mentally be kept separate from itself. The foam structure, or local inclusions, may constrain areas into receiving such matter. And since alveolar cavities, even those of Bütschli's structure are used to hold waste, inutile, and excess, as well as harmful or unsuitable matter, entrance of the latter does not necessarily mean their selection, or even their acceptance, by the living substance. It is to be urged also, that areas which for their guidance in taking up materials depend on certain specialised tactile senses, may be misled through these, whereas further within the cell or organism lie other local specialised centres whose selection may be guided by chemical reactions. What concerns us in all these cases is the subsequent action of the living continuous substance as such, or as organism, with respect to these intrusive things. *It is therefore, not alone physical reception of certain things by protoplasm in areas, which is to be understood as true substance selection, — but the full value of the most intimate processes, and especially the final verdict, of the living substance as such.*

That any nice adjustment of combined chemical and physical conditions must be open to injury from chemical and physical violence — to consequent maladjustment which may become disintegration — is certain. That the living substance as knowable by us expresses an intricate, delicate, and most unstable set of molecular adjustments whose complexity is far beyond our analysis, can hardly be doubted. *Is it not the most noteworthy thing that, in spite of this, it manifests so strong and persistent a hold upon its individuality; that it can withstand such shocks and respond to such innumerable and kaleidoscopic*

shiftings of conditions as often occur inside and outside it, with such plastic unity of phenomena. It is this marvellous maintenance of its selfhood which seems to me more marvellous, more worthy the powers of research workers, than any abnormal states one can force upon the substance by virtue of its conditionings; — especially as amongst the latter we are unable to separate the extrinsic from the intrinsic, — or to say which reaction is due to these, which to those.

[124] Despotic as they seem from a familiar standpoint, the external contact relations of organisms and species are not as a rule the most important division of the sum total of such influences which guide its destiny. They are the conditions least under control, yet they are largely controlled by the substance's use of that other set of environmental conditions which it has gathered together for itself, and by which again it moulds new reactions for its intercourse, as organism as well as substance, with external environment. External environment represents rather *opportunities* for the organized living substance. *Internal environment represents at a given moment not only opportunities but intrinsic necessities for the substance.* That the substance may be, to an important and often to a vital degree, influenced or even domineered over by external environment is indubitable, but to say this is not to say that the latter is its veritable control, or arbiter of its fate. As matters now stand, external environment dominates the living substance only in so far as it denies or inhibits it from using, or perpetuating, its own peculiar and necessary internal environment; and the substance has devised many ways of eluding and defying external conditions in this.

Stimulus from external environment is transitory, while often the substance reaction long outlives it, and that physical organization on which such reaction was effected may outlive both as it preceded both. In gross, the organized powers of the substance as organism are seen to be used chiefly, if not wholly, to obtain for the substance as such the material needed to continue or to produce, physiological function and physiological differentiation. And organization of this environment is secured by contact extension, and by repetition of the same

phenomena, *i.e.*, the selection by the substance of its own specific environment.

[125] This becomes plainer if we turn for a time to consideration of some ways by which the living substance evades, outwits, or defies external environment. In one class of such phenomena, the substance, finding external conditions adverse, simply sends them for the time being "to Coventry," isolating itself more or less completely from all immediate intercourse with them. In the lower forms, even in some so highly organized as rotifers, this action is shown by the habit of encysting. In the higher forms, hibernation expresses the independence of the substance, and in both phenomena the substance shows that it is capable of withdrawing into itself where, by aid of its specific internal conditions, it can sustain the frown of circumstances. Even the rhythmic nature of ingestion acts — which in different organisms cover widely different intervals — is here a most significant phenomenon, and the torpid state of the boa-constrictor (and of many savage peoples) after infrequent meals is but an exaggeration of substance habit which links these acts more clearly together with those whose object more obviously is to render the organism for variable periods independent of its external environment. In many cases and for variable periods, protoplasm itself is used to protect an organism from external conditions, or to render it independent of these. The containing body purveys for and shelters, albeit often unconsciously or unwillingly, the contained body. This is the meaning of parasitism. The same thing is also expressed in most reproduction phenomena, notably in fertilization. Here again the thing of greatest importance to substance life and substance habit of both host and guest in the dual life is their own internal conditions. In such artificial phenomena as grafts of areas and organs also, the substance seems often to live a truly parasitic life, continuing rather to select its environment in accordance with its own accustomed habit, than to yield to the mass character of the host. Curious induced differences in habit of local deposit of reserve material, shown at times in regeneration, may mean a use of inclusions prepared for different emergencies, or, abnormal secretive function in the substance.

[126] Thus much seems certain, that the power of the substance to transport itself by contraction from place to place, either within or without the mass, either as organism or as substance, either as a whole or as portions too minute for us to trace; its power by the same property to subdivide, or consolidate, the alveolar inclusions of all the foam structures we can detect, and to transport them also hither and thither within its mass; and especially the power shown by the substance in its utmost simplicity or complexity of organization known to us, to select its own specific environmental conditions[1]: these things underlie at some point or other of their progress, all the manifold and complex phenomena seen in the animal world.

All the phenomena of egg development seen in the Metazoa as all the phenomena of areal formation in the Protozoa, however fleeting, may be expressed in terms of these results as due to organizing activities of the continuous element, tending always to more radical and sensitive selection of its environmental conditions as a basis for organized activities.

The segregation of yolk and pigment matter to certain areas during larval development, which is so finely shown in rotifer, starfish and echinus eggs as well as in many others; the converse segregation from many eggs with huge yolk masses, of the living substance, thus setting it free for its organizing development, are typical instances of such substance choice of physiological environment. The pursuit of light, heat, oxygen, or of other conditions among the opportunities of external environment show action of the organism as a *procuring device* for the substance as such. The formation of contractile and irritable structures in response to stimulus, as described in a previous section, yields a still larger and more strongly typical, though closely allied, group of phenomena. Though due always to one final cause as stated above, protoplasmic organization and reorganization has two aspects and is brought about in two ways. In one of these, greatest prominence seems to be given a placing of inclusions with respect to the substance,

[1] It is not claimed here that the substance can do this apart from its normal conditions or state of being, therefore experiments upon excised or mutilated portions of cells or areas have no bearing on the question.

and in the other it is a placing of the substance with relation to inclusions, as by migration, subdivision, or extension of the continuous element.

[127] The formation of organized areas, of substance organs and of organism organs; hibernation in all its aspects; motion from place to place in search of food or other environmental conditions which directly or indirectly affect the substance as such; coalescence; conjugation; fertilization; reproduction; the birth of eggs or young; the selection of proper external environment and the preparation of proper internal environment for offspring substance by the parent substance,—as when an Ichneumon pierces a caterpillar, or a beetle rolls up balls of excreta, in which to place its eggs, or when a mammal feeds its offspring with milk:—all these seemingly very diverse phenomena are expressions of one and the same thing, —the selective power and habit of the substance as such and as organism with respect to its specific and necessary environmental conditions.

Nor, as pointed out, do these phenomena differ greatly from ordinary ingestion of food, or daily purveying efforts of the animal. In one case enough is taken for a seemingly secure rhythm of necessity, though a relatively short one, and in the others enough must be secured for a rhythm of privation which it is felt will be a long one.

Among the lower forms, the creature does not seem to need to make special preparation but at any moment can enter upon such states of vital abstraction from external environment. When the organism realizes, or feels, adverse states of surrounding conditions, it simply encysts or seals itself within a more or less impervious covering, and, suspending all action, waits for the proper moment to resume its life as substance machine. Or it throws its resources into the form of young which, from their physical form and physiological state, have far greater resistance to adverse conditions. Watching many of the Protozoa encyst themselves, I have seen a relaxation of the normal alveolar arrangement to be common, so that physiological areas were mingled and the structure of Bütschli became more regular, as in states preceding dissolution. . .

Nothing, I think, shows more clearly that the stable substance as organism is merely a device for securing, and for elaborating and storing the specific environment for the substance as such, and especially for the perpetuation areas of this, than the facts connected with the history of these latter. In the case of development of embryonic forms, we see the organism for long periods wholly independent of external environment as a source of supply, for it bears within itself all that is most essential to its growth, and without which it could not exist at all, no matter how favorable were all external conditions outside the eggshell, or membrane, or jelly-like covering it has been directly or indirectly provided with by the parent organism. And often the parent's own body wall shields and isolates it for long periods.

[128] From the offered standpoint there vanishes that paradoxical mystery which surrounds preparation for larval or adult environmental conditions never experienced by an organism. Such phenomena express a reaction to already existing environment. This is potent before opportunity to use an organ so formed arises, simply because it is in a sense independent of this. Such is the characteristic formation of cilia before the membrane of the egg is broken through; or of a double pellicular plate within the blastomere of an echinus egg before segmentation; akin also is the phenomenon of the beaver building his winter dam with fire-irons on a parlour carpet. It is all to be summed up in the saying that the substance's acts are based on its own internal conditions, and that *all those structures which seem to precede function do not, after all, actually do so, for they are, in the first place, substance organs before they are organism organs.*

Peculiarly is the selection of certain portions of external environment by the organism for the substance as such, a similar manifestation of the same habit as a selection of certain conditions by the substance as organism, either for itself, or for those portions of itself destined as newly incorporated organisms to outlive its older self.

[129] The fact should be kept well in view that, before its separation, an egg or bud has been simply an organized area

of the parent substance, where were gradually segregated from the parental store some precious continuous substance with enough inclusion material of varied nature to serve the latter then and after for variably long periods of its career. Experience of a disconnected set of facts, and a natural inclination to regard the state of being a unit or entity as of more importance than the state of being continuous in kind, or character, with other units; have inclined us to think more often and more strongly of egg and sperm as future but imperfect organisms, than as what would seem to be their still more important character; namely, *areas of differentiation of the parent organism.* Like the lungs, heart, stomach, liver, — or even like the ovary and testis themselves, — they stand structurally for mass organs and for substance organs. And they contain characteristic quantities and distributions of the continuous substance in relation to specific materials. They should, I cannot but believe, be considered more from this point of view to be better understood. It will presently be spoken of how they arrogate to themselves the service of the whole machine and being served to the full extent of the powers of this, or to the satisfaction of their own intrinsic necessities as perpetuation areas, the machine may perish, if no better may be. As the daily, winter, or emergency store of nutriment is laid up for a periodic and rhythmically recurrent or intermittent set of conditions for the organism as a whole, so it is laid up in these areas for a set of conditions which are periodically or rhythmically recurrent in the race-history.

[130] From this standpoint, the organism appears in the guise of a machine or device framed by the substance as such to secure its own specific internal environment; especially to secure this for that phase in which it assumes the rôle of offspring substance. There are frequently large and most complex areas set aside for the function of preparing and selecting from the sum of the parents' internal environment substance needed by the perpetuation or offspring areas. A machine within a machine is formed for use and service of the nursling substance. (See Parasitism, Fosterhood, Heredity.)

The supply by parent organisms of specific internal environ-

ment or conditions for their offspring substance, and their labours to this end, seem still more wonderful when the offspring has undergone complete separation than when it is still an integral part of the parent. I should group the latter cases with those preparations made by the substance as embryo or larva for conditions not as yet unexperienced.

[131] The attitude of the parent organism with respect to its offspring or perpetuation areas is evinced by its often directly renouncing its own specific environment or even its own continued existence for their supply.

[132] A certain control of the living substance by external environment was the great theory set before us by Darwin. Yet it is not control by external environment of the substance as organism, but of internal environment by the substance as such which primarily rules the course of events and rules them most despotically, even to the point of independence and dissociation of the organism from external environment.

[133] Substance habit, which in one aspect may everywhere and at all times be expressed by terms of organization of internal environment with relation to the substance, has always been along lines of increased control, direct or indirect, of external environmental conditions; sometimes by increased differentiation, sometimes, as in certain cases of endoparasital existence, in the direction of greater simplicity of areal differentiation.

[134] In each act of the substance, we cannot escape the preformed machine, but at least in formation of a new machine, or new parts, or rearrangements, of the old, we see each step controlled by activities which seem to transcend the limit of power of the physical and chemical conditions of all visible machinery. All reactions of the organism to environment appear to me to express substance-reaction to pre-existing and specially prepared internal environment; to express the intrinsic powers of the substance under specific stimulus or direction from within rather than from without, — powers which, though they are for us finally inseparable from its physical and chemical composition, are still seen as separate from, and to great extent controlling, these.

Response to environment in character of its own peculiar intrinsic powers, — this is the power of the living substance; and, to repeat a point of radical importance, that response is in character rather than in kind. Sometimes these terms are indeed interchangeable, as when transmissory or sensory areas react to stimulus of activity, as contractility or irritability, of other areas of the living substance. To light, to heat, to impact, to chemical contact, the substance still makes response in character, over and above the immediate physical and chemical reactions which its physical form and chemical constitution necessitate. I have shown that we have at present no right to carry these conditionings so far as to make of this statement a *petitio principii*.

[135] There is now for us a living, irritable, continuous substance of a protoplasmic foam; and there is its environment, internal and external; and these two sets of facts must at all times in our thought of them, as they are in fact, be kept within touch of each other, — never quite separable, yet wholly distinct. It is the living substance in reaction to environment which has made and is still making the whole history of organic creation, — the substance's response to environmental conditions being always in character rather than in kind.

[136] That standpoint which should regard animals or organisms as disjunctive portions of an historically continuous substance — continuous in three dimensions of space, however, not in two; — which should use interaction to internal environment to throw light on interaction of the same substance with external environment; which should in short read the phenomena of the organism to interpret phenomena of the substance, and use these to illuminate those; seems to me the most reasonable. The fact that our eyes look out rather than in, together with great defects of our optical tools, and the general opacity of living masses, have long withheld us from this point of view.

[137] The substance both as organism, and as substance organ, secures so far as may be that which is needful for its energies down to its smallest pellicular subdivisions; and that substance as organism which has best cared for the substance as such, which has best borne neglect or privation inflicted

by external environment, which has been most plastic in its devices and activities, is that which is perpetuated. And its activities are developed by use along these lines. This presents a new aspect of natural selection. It is indeed upon the selective power of the substance as such and as machine that the natural selection of Darwin must act. It must always be accessory after the act rather than an agent in the act, and even habit, individual or inherited, cannot be excepted. Through grasp of this basic fact of substance life, namely, selection of its own specific environment, individual, race and species habits are brought into a more unified and intelligible relation.

The "struggle for existence" remains a struggle for food, using the word in its broadest sense. All struggles of the substance either as such or as organism for place and vantage in external environment as well as for the actual substances it holds, are to this end. Air, light, space, with more subtle conditions hardly yet understood in some cases, are also demanded by the organism because the substance as such requires these for its activities and internal arrangements. In the battle for these, such docile ingenuity and plastic contrivance are displayed by the substance, as more and more amaze research workers. The tendency of evolution seems to have followed lines of strengthening and conserving this aim and need of the Substance, — to control its own environment.

[138] Now food for the organism has commonly been taken to mean actual increment for it, either as new living substance or to replace portions of this which have suffered dissolution supposed to be a necessary result of characteristic activities. Certain remarkable correlations between the waste product, loss of mass or weight in the organism, the amount of energy displayed and the heat generating properties of the food taken in ; have formed the basis for a belief that food is used to repair waste of the actual living substance or to construct new quantities of this. The facts as to structure given here, make it quite possible and even plausible to suppose that we should not with certainty predicate this correlation between chemical and physical expenditure or supply and physiological activity, as meaning destruction or repair of the actual living substance.

We cannot predicate either the constitution or the final action of the living substance. What composes it, or how it grows, or is weakened, or dissolved, seems further from our knowledge than before, because all we have to base any theory on is chemical interactions between substances, none of which we can assert to be the constituents of the actual living substance. All the production of energy, all the waste correlated with it, may belong to the environmental conditions purely of the living substance. Its action upon them and even the waste products of this expenditure of energy may be wholly beyond our analysis. We may not yet have discovered the mode of analysis which can resolve for us these products, — if, even, they are chemical conditions known to us and within reach of our gross handling.

It seems probable from these researches that out of the sum of all the innumerable chemical and physical conditions sought and appropriated by protoplasm, a few certain ones only are needed for actual perpetuation and reconstruction or construction of the living particles, and that the bulk and majority of them are to serve as opportunities and stimulus for its internal powers and activities. It has been stated that owing to the physical form of the substance, growth of living masses can take place to an enormous degree without increase of amount of the actual living substance. Whether or no the living substance itself is renewed by the myriad substances it accumulates within and about it, it is certain that these actually form its specific environment and the sum of the opportunities of its lamellar subdivisions, and that upon the selection and use of these both by the organism and by the minute portions of the protoplasm, depend the normality and organization of its activities and the correlation of its phenomena, — more than this, the preservation of its life. In short, however we decide upon the question raised, the life history of the organism, from the time of its inception as an area of the parent mass, may be expressed in terms of supply for its internal environment. For the intrinsic powers and properties of the visible supposed living substance, are found to be alike wherever it was examined. Its specific areal modifications of function and products are to be taken apart from these.

[139] The whole series of structures which increase the range of organisms' intercourse with external environment, that is, the sensory organs, have peculiar reference to extension of the control of supplies for internal environment. The extension and intensification of irritable reaction, which are seen in the ectosarcal structures of sense organs, practically annihilate distance and bring knowledge of supplies for which, if they must be in actual physical contact, the creature might wait long and perhaps hopelessly. As when a moth is drawn by odours too delicate for our perception, to its mate many yards away; or a wild beast scents its prey, or an eagle marks his quarry, from afar.

[140] According to the kind, and the distribution in environment, of its supplies, the character of the substance organs or structures of the organism are adjusted. In the plant and animal kingdom in their most familiar forms these things are strikingly marked. In both, the same general laws hold good,— that is the organisms select, not only what may serve for immediate use, but what may be laid up for use when the source of supplies is cut off from them, — or so lessened as to threaten the species by too fierce warfare amongst its units for the scant material : In both, the best efforts of the machine are spent for the needs of perpetuation areas: In both, the kind and quantity of the nutriment cause curious differences in the form and character, even the sex, of these areas.

(a) Yet in each kingdom the characteristic choice is along the direction of those elements, or opportunities, surrounding it, the pursuit of which, as well as their chemical constitution when secured, tend to preserve and develope existing types of organisms. And with the character of substance habit in all these things goes the peculiar character of the ectosarcal structures, and the form of the machine as a substance device.

(b) The animal kingdom has chosen the secondary, the uncertain, the motile, scattered, opportunities of environment. The plant kingdom, as a whole, has chosen to develope its powers along the lines of constant, stable, and, one may say, almost omnipresent conditions.

(c) Correlatively, the animal must develope along the lines of contractile and irritable structures, while the plant developes along lines of quiescent, assimilative, vegetative habit, and of chemical reaction.

(d) To the animal, surface is of less importance than the qualitative and quantitative structures developed within the mass. Economy of surface with concentration of powers and function will best serve it in the long run, in dealing with the evasive conditions on which its existence is staked.

(e) In the plant kingdom the substance is extended and organized in such a way as to secure for it as it rests passively in its place the largest possible quantity of light, air, moisture; while its structures are so framed and grouped as to retain and control these supplies. In its reproductive phenomena, we see an approach to the more animal type of structure and function, because the more kinetic element must, like an animal, deal rather as contractile and irritable substance than as assimilative substance with environmental conditions.

(f) On the other hand in the animal kingdom we see often in the female reproductive phenomena a plant-like phase in which the assimilative and quiescent, or vegetative, state predominates.

(g) In plants there seems to be chiefly a quantitative extension of function during growth and development. In animals while the powers advance along paths of both quantitative and qualitative emphasis during growth of the individual, the qualitative emphasis is usually most notable.

(h) In both kingdoms the full set of intrinsic powers of the substance seems to be alike and to be in great measure retained; but their habitual expression differs in the two. Just as in the animal there are purely vegetative and assimilative areas, so in the plant there are markedly contractile, and in most, irritable states also, of the protoplasm. Indeed, in each cell area of both animal and plant these truths are characteristically repeated.

(i) The extension of the animal's control over external conditions by means of its intensification areas will be discussed in full both as to means and manner, in my forthcoming paper.

(j) In the plant kingdom, the extra hoards of internal conditions become more rigidly adjusted to known rhythms of supply so that, as a rule, plant individuals are more readily and radically damaged by sudden environmental adversity than the animal units are apt to be, the habits of the latter being adjusted to meet intermittence in habitual sources of supply.

It has been impossible because of rigidly limited space, to do more than indicate in this section the leading lines of argument, and grouping of facts which have offered the standpoint discussed. Here too, as throughout the article, I have preferred to use as evidence so far as possible phenomena observed personally, although there are innumerable established facts which might be cited, and the reader will, it is thought, find in his own mind stores of added confirmation.

[141] To sum up in a few words the gist of what I have striven to make clear: The living substance down to its final visible subdivisions is seen everywhere seeking or selecting its own environment. All its guises and aspects, all its phases and phenomena are to this end; and chiefly that the perpetuation areas shall be supplied with such environmental substances as will render them for long periods independent of the chances of external environment and then leave them prepared to resume the struggle for other similar areas in turn.

[142] That so potent and radical a function of the substance should have areas of differentiation devoted to it, that it should have given rise to substance organs, or centres of such control, would seem a most natural thing. I believe that such organs were, indeed, among the earliest formed of all areas of differentiation, — excepting simple ectosarc. They are distributed through all living masses at short intervals, the first care of the substance in increasing its mass to any extent, or in increasing its scheme of areal differentiation, seeming to be to secure repetitions of just such centres of control or substance organs, and the surrounding substance in many cases, perhaps in most, seems to have lost the power to do without them, — just as a mammal has lost the power to do without its heart or lungs. I refer of course to the nuclei. Up to the present time there is ever-increasing evidence that they may rightly be

assumed to be selective organs for the substance, that is nutriment control areas. Whether these areas are this only or whether they serve also as substance ganglia, carry the form and function memory of the substance as such and stand for the nervous centre or brain of the cell area, must rest for future research, but the facts which connect them both with the cytoplasmic granules and with nervous structures have been pointed out earlier in the article.

Parasitism.

[143] I have said that many areas which as substance organs function markedly for organized contractility or irritability, are formed of more or less unstably segregated protoplasm in which the alveolar inclusions of the actively functioning substance are uniformly fluid. These inclusion fluids are carried from assimilating portions of the general substance, or received by dialysis, or even from wandering interalveolar foam. Such areas depend upon assimilative areas for their special environment. To this extent they are parasitic. Whether they in their turn serve assimilative areas directly with their products, or indirectly by their activities, is aside from the immediate issue. Much interalveolar substance of Bütschli's structure forms a constant typical area of this sort. Parasitism is used here, in that broader, more genial, sense which does not preclude the idea of mutual benefits between dependent and supporting areas. In such organisms as amœba where function and structure seem alike interchangeable, the substance forming true ectosarc may but a short time before have taken part in active assimilation areas, and even where ectosarc is a quite stable formation, its interalveolar foam may pass as an active carrier to and from these. By watching for hours the progress of assimilation in Protozoa, I have many times seen that there is at intervals a determination of fluid in considerable amounts to the food sacs — the temporary stomachs ; and again a sudden redistribution at intervals, or a more or less steady draining, of fluids from such sacs into the surrounding protoplasm. These phenomena are mingled

with flux of Bütschli's structure and of interalveolar foam. Even in organisms having complex vascular systems, the work of these must be supplemented by just such minor or more primary dissemination processes, in order to reach areas whose continuous stuff has no immediate contact with vascular currents. For much protoplasm in every organism, the continuous substance, as alveolar lamellæ and as interalveolar channels, currents, and filose processes, both physically and physiologically carries on this work, — which means to the substance as such just what the grosser vascular systems mean to the organism.

Every new formation of ectosarc however fleeting extends the parasitism of the substance as such. And every new area producing, or segregating, materials needed for contractile or irritable function of the substance elsewhere, acts as a device to furnish parasitic areas with their specific environment, that is, with their intimate opportunities, or causative conditioning. Besides that physical restraint which the presence of more solid inclusion matter may cause the contractile powers of the substance ; secretions, or chemical processes of primary digestion may also to some extent restrain, inhibit, or intermit these. They may be necessarily alternative or secondary results. The converse may also be true. With regard to Bütschli's structure, ectosarcal areas stand often for secretory habits of more or less pronounced character, for in this structure, as stated before, all sorts of materials are deposited, and an organized number of vesicles having kindred deposits would mean, or indicate, a local habit of the general substance as such. If fluid, such deposits form physical opportunity for organized contractile and irritable function. In other cases these inclusions may serve to inhibit characteristic activities of the substance, and then this will commonly be withdrawn by degrees to more free conditions. In many cases parasitic areas take from the general store, or from special areas, matter which is useless or positively hurtful to the substance, or which is to be transported elsewhere, or held in constraint for coming substance organs. (See Heredity.) Such are many wandering cells of Metazoan systems. These

have a curious individuality of their own, — they are like organisms within the mass and act as carriers with such seeming sentience, with so surprising a sympathy of response to a host of internal needs and states of the general substance that it is only when one looks at them as *free connective tissue areas* that one can at all understand their relations to and with the general substance. Such service as they yield in grosser expression is supplied the substance as such more radically by migrant currents, by filose processes, and perhaps by chemical or physical conditions. I have watched *in situ* in soft shelled crabs, certain of the leucocytes take the form of bi-flagellate monads with variably protoplastic posterior region, and travel about thus, constantly insinuating with some appearance of force the tip of their long flagellæ which were sharply pointed, into the tissues about them. Whether they brought substances or took them away or stimulated excretion from these tissues could not be seen. One would perhaps think them parasitic forms were it not for their frequent metamorphoses. In blood drawn from the crab they quickly change to the Heliozoan like state and aid in the coagulation phenomena.

[144] Amongst organisms examined, from Protoplasta to highly organized Metazoa, the complexity and number of areas laid down for organized contractility and irritability appeared to be correlated with number and complexity of devices for assimilating, and for transforming assimilation products into most varied materials, all of which when presented to the substance as such were in dialysible form. (The male rotifer and similar cases, as of spermatozoa, do not form a true exception here, — see following sections.) *Looked at from this standpoint, cell division, and, more broadly yet, areal differentiation appears as chiefly a multiplication of ectosarcal areas or organs and, with this, of a nuclear machinery to control their specific supplies.*

Parasitism of the substance being an established substance habit, it like all other such appears throughout the manifold relations of the substance as organism. And here, as in other substance habits, there is in higher organisms progressive increase and extension of it in all the relations of the sub-

stance. Such parasitism as does not belong with phenomena of true fosterhood may arise in varied ways. It may occur either as direct selection of another animal as a chosen source of supply, or accidentally from ingestion of one organism by another. The organism so ingested may find its new surroundings so much to its purposes, that is, so much in accord with established substance habits and organs of its own, that, far from succumbing and becoming chemically disintegrated, it is as it were enclosed in a factory or source of artificial supply. Instead of serving as food for its captor, it uses the latter either as endosarc, or purveyor organ, or actually and directly as living food — devouring its tissues. Or, it may pass to some special area and there merely filch from the prepared or selected food what its own uses require. It is not strange that under such circumstances the plastic substance should lay aside or modify substance organs for securing and preparing its food, while retaining and accentuating those which best fit in with its new set of opportunities and compulsions. In a retention of their own individuality by grafts or transplanted structures, one sees that part of an organism may continue to maintain its selfhood while fed by another organism, of which by substance parasitism it becomes physically an integral part. *It shows again the importance of the substance as such, and that the local form is not merely part of a whole organism as such, but primarily and radically an expression of substance habit.* (See Heredity.) Such facts throw light also upon the physiological differentiation of substance organs with continuity of a physical and physiological nature between them.

[145] Once established as dependent, the parasitic substance, whatever its habit, forces the supporting substance or organism to play the part of foster parent and itself resumes a rôle which as fosterling substance, or perpetuation area, it once played. For among all the multiplex dependent areas, those most unmitigatedly parasitic and exacting are the perpetuation or offspring areas. By a parasitism which is in harmony with its fundamental structures and habit, or which releases it temporarily from great enforced strain of its condi-

tionings, or which enables it to make fuller use of these, the substance as such and as organism seems to profit in renewed vitality. These conditions are to be found very commonly alternating with converse states of initiative activity of both the substance and its gross expression in organisms. The more vicarious means of supply can be extended, the more the substance may expand and expend its own peculiar powers in self-expression. But unless states in which an endosarcal set of habits are peculiarly fostered alternate with ectosarcal self-expression the organism or area becomes by so much degenerate; and if the latter outrun the former it becomes exhausted. The value of such alternation is probably at the root of that flux of living substance in organisms which has been so much emphasized throughout this paper. Here again one sees substance habit and its conditionings apply to organs and to organisms —*peculiarly in reproduction phenomena.*

Fosterhood.

[146] The word parasitic having by a certain frequent use associations which in some connections are jarring, it should suffer as idea a transformation of verbal form gracious enough to follow that of the fact into the beautiful phenomena of parenthood. Dependent perpetuation areas may be called fosterling areas; the supporting substance foster substance, area, organ, or organism. Of all areas differentiated to live at expense of other parts of an organism, there are none so grossly egotistic, none which so take all and keep all for themselves as the perpetuation or fosterling areas. From their inception, for variable periods, often covering the whole term of their existence, they receive largely from the foster substance in many of its phases. It is common for a parent organism to support a special machinery whose work is alone for the offspring area. The whole parent itself as organism may be regarded as serving as a substance device for securing and preparing the materials needed by the perpetuation substance. For the pampered fosterling areas the rest of the substance may go more or less lean and hungry. To them

may be sacrificed not only the general mother substance but the father organism also; more than this, many potential fathers may perish in warfare merely that one such area shall have the best of the material it needs. There are even cases in which the entire father organism is but a servant area for the fosterling substance, having existence, and possessing no other parts and powers, than are necessary for this end only. It is but the sham of an individual, neither eating nor seeking food for itself. It acts only to secure for the perpetuation substance it carries in the form of sperm, certain specific environment this needs. It is a messenger foster area of the mother organism. All its structures are adapted to this service and it is an emphasized expression of the true meaning of perpetuation machinery and areas. Such are male rotifers, — they pass through an egg phase but remain free swimming foster areas of the mother organism. They never advance beyond a true parasitic state, — they live and move wholly by the specific environment the mother machine stored up within them, and they perish shortly after accomplishing their mission, that is when the sperm has been deposited within the body cavity of the mother through a hole the tale spike of the male pierces through the body wall usually about the shoulder region. They possess no means of receiving or assimilating food, are chiefly if not wholly ectosarcal, and are largely motile, tactile, and perceptive areas. They have, let me repeat, no true self expression as individuals, not even the semblance of it common to organisms; they function wholly as separate areas of the mother rotifer—and for the race. They seem to me from a hundred facets to illuminate the place of the individual in the history of the substance. They form also a fine illustration of the extent to which what one might term *vorsichtigkeit* of the substance extends. A whole generation, speaking from the usual standpoint, is interjected by way of providing that next the mother generation with all its material, for the sperm go to perfect a generation which will be truly collateral with that formed by the males themselves. This would greatly disturb a genealogical record, for the child of one parent seems to be the grandchild of the other. In such a case the male is doubly

parasitic upon the mother generation, — as a free perpetuation machine, and for the sperm (which does not truly belong to the male) and for specific environment for its future development and life. As stated in a preceding section, the male element is largely dependent always upon the female for its specific environment. Other points of extreme interest in connection with the male rotifers are these. They are formed of eggs about one sixth only the bulk of ordinary parthenogenetic eggs producing females; they are produced about six times as fast; they are formed at times when the supply of food is threatened by climatic changes and when the parent organisms need all their reserve stores for formation of the huge winter egg which is fully six times the bulk of the usual summer egg. The male does not even diminish the possible food supply for the parents since it does not, so far as known, ingest. All these facts seem to me to make clearer the true relation of organisms to the race history of the substance, and of ectosarcal areas to substance habit. The facts were personally observed in a number of forms but most continuously and repeatedly studied for a number of years in *Megalotrocha alba* and *M. sp. ig.*

[147] An enormous proportion of the habits and instincts of the whole living kingdom exist in relation to fosterhood phenomena, especially with regard to the perpetuation areas. Among the lower forms are many which retain for variably long periods, or always, vital protoplasmic connection with their fosterling areas even after these are manifestly self supporting. Now just as, by qualitative extension or intensification of the irritability of the living substance, more primary organs of gross and direct contact found in lower forms are transformed among the higher animals into space-bridging organs of sense perception; so here again the same phenomenon of transmutation of structure and function is repeated. Long after actual space and time separation the parent can thus extend recognition and assistance to its fosterling substance and still continue to subsidize its own supplies or functions.

Heredity.

[148] [1] Up to this point it has been cumulatively shown that cell phenomena are underlain by such phenomena of the continuous substance as would seem to inhibit us from using cells, even broadly, as primary units of physiological organization ;— the new facts urging us to trace substance phenomena in a physical and physiological continuity throughout all parts of organisms ; to ignore cell limits, except as they fall within this interpretation ; to see in cell walls and in nuclei local and even temporary substance organs belonging primarily to the mass and but secondarily to cells, their curious repetition being taken in relation to general needs of the substance as such rather than as parts of cells as units of structure ;—*in short to study cells as localities in a mass organization of the continuous substance and as local expressions of substance habit in a significantly common grouping.* From this standpoint and by use of the naïve method of thought approach, the grosser organs and structures of organisms become replaced by an intricate maze or web of substance organs. Organs no longer appear as compounds of certain different sorts of cells, but as a complex of minute substance organs whose multiplication baffles even the imagination, for they not only extend in a lessening series into the invisible subdivisions of the continuous substance but are constantly being transmuted into new structures.

The physical form of the contractile irritable substance offers peculiar opportunities for physical organization, for each vesicle is a nucleus of varied causative power and may form in the series of emulsive foams a radiating centre of influence along several, or along many, lines of continuous substance and of vesicles. Each local aggregate of inclusion fluids of kindred sorts forms at once a true substance organ whose possible structural and functional values are many. The physical form of the living substance of itself may be said to initiate or even compel a formation of substance organs, the chemical nature of the constituents to extend and qualify this natural compulsion, while activities of the living matter may expand,

[1] **Whole section to be read under this number.**

modify and restrain, or with aid of the mechanical conditions may freely form other such organs. The minutest of substance organs, whatever their origin, express potent specific conditionings for living lamellar films and foams. Other areas directly or indirectly profiting in any manner by them, they acquire the value of organs of the general substance ; the mass becomes functionally, as it is structurally, enriched ; the organism becomes, though perhaps but fleetingly, by so much more an organism. In more stable retention, in maintenance or iteration, in multiplication and in varied extension of substance organs, the structures and organs of organisms as familiarly known to us have their birth. These latter groupings come secondarily, incidentally as it were, to form and to belong to what is commonly known as the organism. They were and are primarily for the substance as such. I believe it may be said of substance organs ; they are, — therefore the grosser organs, — therefore the organism. Through unity and harmony of form and interrelation of function in substance organs, and through secondarily acquired interdependence of their compounds, there arises a most specious seeming of prime end or motive in these latter, and especially in the organism they form. (See Habit.)

But besides being structural complexes, organisms are, even more, functional complexes. From the same standpoint and using the same method of approach, an organism expresses itself functionally as a maze of sequent phases, composed at a given moment of many lines of phenomena which are in closely interwoven extension, and even anastomosis, in three dimensions of space. The life history of cells and again that of organisms and still again that of the race, repeat in grosser terms the same truth. Of minute groupings of function in substance organs are built up all the functions of cells, of organs and of organisms. But the complexity of these outruns structure many times, for a given vesicular structure may be the seat and cause of, or opportunity for, many diverse sorts of function. Physical conditions due to mode of lamellar distribution can alone give rise to one set of phenomena, chemical interactions may be manifold and either or both of

these sets of phenomena may be locally isolated or have important relations with other substance organs. These physical and chemical activities may alternate with, or be controlled or pretermitted by, physiological activities which may also make large use of them as opportunities. Of causative interactions amongst any one alone of these sorts of phenomena, volumes might be written, and still incalculably much remain for coming centuries of research workers to write; — and all three sorts are actually interwoven and mutually transmutable as cause and effect.

Constant watching of function in the living substance gave the following results. The function of any substance organ would seem not to be due to peculiar powers or properties of a locally segregated portion of an organism's substance; but to exist as specific temporary relations of a universally similar substance with its specific conditionings. All the facts gathered as to structure and habit of the living substance seem to me to indicate that it is indeed identical in powers at all points in organisms; such seeming differences as it shows expressing for the general substance, local habit of selection, organization and use of chemical opportunities or inclusion material in relation to itself; and for the local substance, specific chemical, physical, and physiological relations with these, influenced more or less by various controls due to function of other areas. Endosarc becomes ectosarc and there functions in character of that mode of organization and opportunities. Ectosarc returns to endosarcal areas to function there again in character of the latter. These things are true of the substance composing higher organisms too, for even here the substance was seen to exchange special organized states or conditions for those more primitive; and, correlatively, its functions for more primal habits of activity. This truth is already partially known in a grosser form of its expression as a "conversion of function" in organs; but in the basis of these, in the true substance organs, it is almost, perhaps quite, universal. I have shown that in minuter structures the substance is in a state of local flux, and that stability of visible structures is but a mask for mutability and mutations of both function and finer struc-

tures ; also that such stable differences as are had by staining reactions are attributable, in the continuous substance as well as in Bütschli's structure, to differences of inclusions and of physical states of the lamellar substance, rather than to chemical differences in the true protoplasm. The continuous substance of contractile or irritable organization, functions often in secretory or excretory manner as well, and in addition to its organized modes of expression, frequently intermits these for, or mingles them with, primitive protoplastic manifestations. The migrant protoplastic substance can maintain the finest visible substance organs while yet retaining diverse other characteristic modes of function. Organs, as we have known them, are expressions of the living substance in some particular way, or ways, but with enormous reservations of power and possibility. Structure as hitherto known, seen thus, takes on the aspect of locally maintained deposits of specific inclusion matter. Function expresses certain local or general habits of the continuous substance with respect to or in relation with these materials. Manifestly, in, and by, no known structure, is the substance expressing at a given moment its full powers, or asserting a prime local difference in itself. The utmost expressed thus, is mass habit of local deposit and use of certain materials, and within this expression is still a wide range of structural and functional difference and variation, not only in individuals of one family, but in each unit from moment to moment.

Another thing of note is that the living continuous substance organism ignores, transcends, controls, and rules, as well as directly responds to, its internal opportunities in any visible structure just as does the organism as such in relation to its external opportunities. The continuous substance follows internal controls and promptings not to be associated wholly with, or wholly accounted for by, any structure we can trace ; it functions according to suggestion or control of more intimate conditionings, — yet always in such a manner as to repeat in its true activities the phenomena seen to be associated in visible structures with vesicular modes of organization of the elements. These intimate conditionings are variously derived and may give rise to yet others.

Most important of all does it seem, that the function of all substance organs, simple and compound, is more or less intermittent, evanescent or recurrent, the recurrence having commonly a rhythm which may be for the local organ statedly self-supporting, statedly dependent, or uncertain because contingent on uncertain aid from within or without. Separating out from the continuous network of phases, those lines or rhythmic modulations formed by linkedly recurrent phenomena, they too weave in substance life history a coarser web or maze of sequences and inter-relations. Sequence lines of minute substance phenomena form part of larger rhythms, these in their turn create still broader organic inter-relations. Each phenomenon of the local substance organ is not in each for itself alone but for all relations with other parts of the vesicular organism. Again, each phenomenon is not for immediate time alone but may be vitally, or indirectly, causative or restraining for remote as well as for directly sequent phenomena. Often numbers of other linked or associated phenomena must arise and pass before its fulfilment is ripe. The end of any substance organ and its function may lie in the developmental history of a coming generation, or even of several generations in advance, for the linked causal nature of substance phenomena is very far reaching. Direct results of physiological activity may have a purely physical or chemical value, or both, and from these again may be built up new physiological manifestations. Whatever its origin,—to what end a substance organ of minute extent and simplest vesicular organization is to function, or by, or through, what remote substance activity it has been prompted, must at all times be in full beyond the grasp of the wisest man. No matter where situated, nor within the limits of what broadly marked organ of the organism it may lie, it may have, or be, a remote result or cause, having little actually to do with its immediate functional surroundings. The instability of substance organization and the migrant protoplastic nature and habit of the substance alone make clear that results or products of local structure and function cannot be limited in sequent effects to the same locality. There is also much distribution of local products of

organization throughout all living masses. It is certain that the local functions of the substance belong not alone to the locality, not alone to the cell, not alone to the tissue or organ, — but to the mass; and again that they belong not alone to this, or even to its direct descendants, or to the family, but to the race. It is the life history alone of the substance as race substance that can reveal the full significance of even fleeting local organizations.

With all its complex interrelations which seem to form so complete a cycle, the individual is in truth but a fragmentary part of a vast complex modulation of structure and function. However separate as mass from its race relatives, it is absolutely inseparable as part of the web of sequence in race phenomena. The strange incomplete, yet redundant, complexity of sequence we call an organism, is, as pointed out earlier, but a ceaseless becoming, of which the adult, or all stages, form a recurrent grouping of phenomena — a kind of rhythmic wave in continuous habit. It is thoroughly transitional, for in it nothing truly begins, and nothing truly ends. But the being is more obvious than the becoming; the structures and phases when viewed in gross appear more stable than evanescent; — and so the gross result produced upon our perceptions is a kind of typical stability or homogeneity. What is seen and described at any given time is, however, a net result of composite impressions beyond our analysis. Form and structure are as much illusions born of our own limitations of perception as has been our conventional mode of seeing and representing apparent modes of motion. Thus have arisen our types, by convention, and yet in a true way after all, *if thoroughly understood to be symbolic*. The form of flame, or wave, or fountain can be characteristically expressed spite of all the local evanescence of forming substance. But this is form symbol, not form fact. Just as in Protozoa a characteristic form or forms, with general relations of parts, is maintained in the mass notwithstanding ceaseless flux of formative substance, so is it in all organisms, only, in most, the structures and phenomena which control our attention and the grosser interdependences of these are less patently unstable. And it must be remembered that with the

same powers required to see the flux of Protozoan forms, the flux of substance in Metazoan forms can also, with greater patience, be observed. Within and through the most complex mechanism of cells, the continuous substance or formative agent moves restlessly to and fro expressing itself as living foam in countless different ways. Primarily protoplastic, it builds up in relative localities of living masses specific deposits of non-living material and maintains these in a general way, without for the most part hampering its total liberty, merely using them to make itself more free in and for self-expression. In developmental phenomena, one sees the machinery of the embryo formed by successive progressive shufflings of inclusions already placed in it, and by more and more searching rearrangements of these in relation to delicate pellicular membranes of its living continuous substance. As differentiation advances, area after area becomes markedly possessed, though more or less unstably, of its own specific inclusions and certain substances become wholly restricted for variable times to certain cell areas or to minuter areas within these. Nuclear division phenomena seem to me to stand for subdivision of specific conditioning material, for repetition of a local control machinery having to do with general needs of the substance. Whether as a ganglion or as nutritive control it is not possible as yet to say certainly. Probably as both.

The life history of perpetuation areas, their dependent relation to the foster machine or organism; their relative importance in time of famine as compared with other areas all clamorous for food; their long periods of reaction to the internal environment provided for them; their relative vigour and vital power as compared with the parent organism when first completed for self-support, or before this even; — all these things seem to me to declare that in these areas the living substance is kept young or re-invigourated by sparing it for a time all wasting activities and by feeding and cherishing it in all ways, even if to do this be to sacrifice the parent machine. *The business of the substance is, after all, self-continuation, rather than continuation or reproduction of an existing grosser organism, which is but incidental to its prime habits.*

The formation and storing of perpetuation areas represents no break or radical difference in the general habit of the mass substance. It is to be remembered that food secured by the organism is always for activities of the future, for even remote contingencies as well as for immediate or certain rhythmic needs. That some of these needs will not arise till a portion of the existing mass shall be leading an independent existence matters little, for the sequence of structures and especially of function has still for this a certain and a true continuity. Considerable interval must always elapse after taking food before the general and local substance has use of it. A storing of perpetuation areas with specific environmental conditions needed for its sequent phases and phenomena is, therefore, one with all the phenomena of distribution of materials throughout the mass, one with all preparation made by a larval stage for other larval, or for adult stages. And indeed the "adult" stage in many cases becomes absolutely parasitic upon the "larval" stage. In such cases it is the whole and not merely a portion of the mass that becomes fosterling, for which the precedent phase acts as foster parent. Some adult phases are as absolutely dependent on this as the ovum is upon the mother organism. In pupa states again, the whole organism passes through an egg-like phase, becoming regenerate and transformed. The male rotifer must again be cited in this connection as an illuminating form. By regarding the organism as a recurrent grouping of substance organs and substance functionings, — as a rhythmic set of substance habits, — the whole living universe comes more within one's comprehension, because expressed in more unifying terms.

But it is manifest that while the creature we know, is built up of substance organs, it can hardly be taken to be by itself the whole meaning, a mere summation of those found in it. In each organism there are probably vast numbers of true substance organs existing and functioning with little or no reference to it, except as they are indirectly dependent upon it as general purveyor. Each of these may represent some attained end or cast-off function which will disappear — vanishing characters in process of elimination from the race

history; some initiative characters one day to mark a new species — incidental but potent beginnings; some dying results of exhausted or unused opportunities; some products of an overloaded, overstimulated state which will suffer readjustment; — any of these things each may be. Whether an evanescent possibility, or initiative of some new series of fruitful structural deviations, whether to be used by the substance as a physical lever, a chemical cause, or perhaps as a mere storehouse of opportunities, or prison for adverse or detrimental influences; — such is in each case, and in each moment with respect to the same vesicular structure, our problem. One may be watching the last falling leaf of some great tree of biological sequence, or the forming of embryonic leaf and root of another such. The organism would seem to be more than we have thought it and less than we have taken it to be. It is an incident rather than an end, but as incident far more marvellous and comprehensible than as prime end. A most complex and compound race organ, it represents a recurrent grouping of substance habits as to local deposit of material and local relations with these. Of such are formed all likenesses of character between organisms and their grosser structures; likewise all differences whether of individual, species, genus, family or race. But within the limits of the most closely resembling descendants there is room for enormous variation, as well as of mere diversity of substance organs, both as to their extension and complexity, without possibility of our detection as yet. Possibly in many cases without any essential difference resulting. This is, it seems to me, a most natural result of the mode of organization and growth. Of such of these variations as best fall in with the opportunities of the organism as race organ and race substance, of such as least interfere with, are most closely allied to, or most in harmony with, established tendencies of race rhythms as well as those of the individual, with latent as well as with patent lines of substance phenomena; grosser variations will probably be built up. For thus, it seems to me, natural selection must act. As substance organs arising from mere physical incident can become true mass organs, so the organism arising from

actions and interactions incidental to aggregate substance organs, can become a race organ. Considering the strange unlikeness between different phases of the same unit, and that of sexes to each other; the marvellous metamorphoses also common; the alternation of generations; the single, dual, triplex, or multiplex, relation of parent and offspring organisms with their common and enormous differences; the colonial and social groupings of diverse creatures; — the place of the unit becomes, I think, unmistakably that of a certain organ of the race substance, incidental to the race history of that substance. Such structural and organic basis as has been used for grouping animals, now seems gross indeed when brought into contact with true substance organs and structures. The difficulty of understanding how organs which could not be of use to the organism until already far advanced could be built up by natural selection, is thus lessened, for they are to be thought of first as substance organs and then as organism organs. And their function in these two capacities may often be widely different. We may know, it may be patent, how any group of substance organs serves the organism as such, or acts in a group of interrelations between its parts; but we cannot be therefore sure that we understand what part this organ plays in the life history of the substance, especially as race substance.

Likeness of the adult offspring to the immediate parent was so common a phenomenon in most accessible groups of beings that it assumed at once in man's mind an undue importance which it has ever since by tradition retained. It is rather incidental than of prime importance except as a general expression of certain broad recurrent groupings of substance habit to form a race organ. A useful fact — and one that has in general looked like a final fact when the history of units was regarded — it has seemed indeed to be an end to which all the wealth of power and adjustment known in the organism was straining. To say that it is a natural and necessary result of the fact that the same powers which formed the parent are in operation at its birth, would be, I think, an inadequate statement, for it may be a result of powers and processes which were wholly or largely in abeyance when the parent was

formed, and the powers and processes which formed both it and the parent are by no means to be limited or defined by those results, nor have they thus wholly expressed themselves. The individual may rather be said to be one recurrent result of conditions that guide substance habits along lines producing race history. The rhythm of that recurrence may in all or a variable number of its parts include many generations. Atavism as commonly known is but a grosser expression of this truth about substance habit. The father element contributes his portion of the web of phenomena of substance habit and substance opportunity; the mother hers. Both doubtless contribute some of each sort of conditions as well as of living substance, but the mother, as a rule, patently supplies most of the immediate inclusion opportunities. Sex is determined, it seems to me, at some variable time by existing internal opportunities which decide the sort of race organ most possible, or most in harmony with these. The race organ has other meaning than immediate self-expression of the substance, but has also its relations to existing external opportunities as well as internal and these become known to and recognized by the sentient mass substance.

From this standpoint one no longer thinks of "transmission" but of *transitions;* one no longer wrestles as Jacob with the angel, with the problem of transplantation and distribution of representative and determinant biophores, — but one sees spread out before one, sequence of phases and phenomena, origin and maintenance of substance organs and substance habit, and the maze of intermittent or recurrent rhythms these form; — one sees the whole race history of the substance as a vast, web-like, compound grouping of physiological as well as physical and chemical phenomena, in three dimensions of space. The individual becomes a single chord in a great orchestral symphony. At this standpoint one finds oneself suddenly relieved of the burden of mental necessity or yearning for any theory of heredity, for such "heredity" appears here to be but a phantom difficulty, a result of artificial separation of portions of the web of sequences, a term forced upon us by an inherited standpoint from whose necessary limitations we have suffered

If the difficulty does not truly disappear as it seems to do, at least it no longer stands between one and simple organized effort, it no longer thrusts itself between one and the subject. Here, it seems less urgently necessary to speculate of the how of heredity, than to watch the living substance and learn its varied sequences of self-expression.

Habit.

[149] To substance habit, then, must we look for all likenesses and differences found in living organisms. This might seem merely an exchange of terms, leaving the root difficulty untouched, were it not that our new facts make it possible to separate habit into more fundamental sets of conditions and functions; and this is useful, for, in the substance as such as well as in the organism, habit is a most complex state of things.[1] In terms of my results habit of the living substance in all its relations may be described thus:

Habit expresses certain characteristic vesicular groupings of the living and non-living elements of protoplasm; it expresses also any or all iterated or characteristic primary, secondary, or remotely linked, interactions of these conditions amongst themselves, or with any existing opportunities, compulsions, or stimuli within or without the mass or area; it can also mean simply a state of actual or cumulative preparation, with intrinsic powers, for such interaction whenever it shall become possible.

Protoplasm in which no structure beyond a nucleus is seen, is commonly called "undifferentiated" or "the simplest form of organism." All visible structures and their associated functions, all visible activities of mass or area, we are used mentally to bestow upon or refer to the "organism." When, for instance, the cuticular alveolar layer of a Vorticella responds with organized contraction to local stimulus, we say 'the Vorticella contracts,' just as when a dog's leg moves we say 'the dog moves his leg.' Because cuticular contraction often removes the Vorticella from harm's way it has seemed

[1] Organism will now be used in a limited sense to imply only those parts and functional interrelations heretofore familiar to us under that name.

a purposive habit controlled by the organism. By changing this standpoint,—by taking structure and functions of vesicular organs in their relation to the substance as such and to each other as organs of this, — much will be gained. In any visible structure the continuous substance is a protoplasmic foam. From or through this must the coarser vesicular inclusions be built up and maintained, either chemically *in situ* by the local substance, or as deposited products of the general substance, brought, it may be, from some distance by physical or physiological agency; they may also be caused by aggregation of minuter vesicles, or by their bursting into each other; or by protoplastic activities. Except where formed by direct protoplastic ingestion, they are modifications of existing minuter inclusions; in all cases they are due to functions of the finer foam. Being products of a more primary set of structures and functions they are secondary in origin and may be purely incidental to the more intimate and basic life history and habit of the continuous substance.

Once formed, each new series of vesicular inclusions necessarily introduces new interactions and new interrelations, chemical, physical and physiological. These can create for the mass such functional possibilities as may materially alter its habits as organism. For instance, while the finer foam carries what can for relatively short periods maintain its functional activities, a fluid structure of Bütschli whose inclusions are of reserve similar material, can make the general or local substance independent of renewed appeal to external environment for much longer periods. Such a structure by receiving excretions as well as excess of specific nutriment or stimulus can also prevent clogging, or impeding, or functional waste, of the active substance, and can save loss of time, force and substance in deportation by interalveolar currents. It is a conserver of established habits as well as an initiator of a new series of functional relations. It offers increased leverage, and opportunity for organization of contractile powers on such a scale as can more patently alter shape or displace a mass or area. It keeps together relatively large quantities of substances secreted or excreted by the general substance or pro-

duced *in situ*, so that these, when poured out at intervals, can by their quantity strongly influence other relatively large areas, or similar organs on an equal vesicular scale. It represents naturally a certain decrease of osmotic compulsion, and of lamellar tension and mass viscosity, and greater economy of lamellar material with reservation of its stimulus. Its inclusions both by the physical opportunity and compulsions they offer, and by the chemical interactions they supply and create, serve indubitably to maintain the local and general substance in functional activity. Thus they come to mean reserves or grosser conditionings on which life and habit of the race substance can depend. Such an alveolar structure alters and influences functional rhythms. Possibilities of substance parasitism are much increased by it, and this is of radical importance. Such a structure means again, increase of mass with many fruitful chemical and physical relations which can materially affect the fate of organisms. Above all, it offers opportunities for sudden irritable and contractile organization of specific sorts; and for sudden intensification of the powers of the substance, as well as of swift recuperation and nutrition or stimulation for this, since formation of a finely subdivided foam from a structure of Bütschli, brings at once into play an immense amount of reserve material and in such a manner as to yield at a given moment stimulus and food to the largest area of irritable substance. Basis for organized response as well as nutrition and stimulus can thus be swiftly and enormously increased within a given space limit. Since this change takes place in the finer foam also, it is clear that even there, resources over and above those for immediate function are carried. I have already shown that formation and physical modification of ectosarcal areas must have a powerful effect on form, motions, and ingesting habit, besides exerting a radical guidance of the general habits and instincts, of organisms. Since a mere physical incident of local segregation of fluid-bearing alveoli, offers the contractile, irritable, substance opportunity for organized function of various sorts, it seems the physical form alone of protoplasm may have been a potent, and even a cogent, factor in evolution of organisms along lines

leading into expansion, extension and intensification of the powers of the substance; — that is, it may have opened the way to, or even enforced, an ectosarcal set of substance habits. Much stress has been already laid upon formation and function of ectosarcal areas. They are indeed of almost unbounded importance in the history of the substance and organisms. Through these areas alone does the substance attain its most complete control of environment; through these alone it structurally reaches its higher life of the senses, of perception, of thought, of psychological growth and reach of function, all of which things are rooted in vesicular organization of irritability and contractility; — for in these areas the living substance is set free, fed, and stimulated, for fullest, highest and most characteristic self-expression.

A single vesicle of the structure of Bütschli forms for the continuous substance a true organ, and when there are many whose interactions of causes and opportunities make up an organ, or set of functions, useful to the general substance organism, — there has been formed within the mass a secondary organism. However incidental their origin, each set of functional interrelations extends and conditions and makes more dependent the true primary substance organism, and, as we have known, may even obscure this as cause and end. In numerous ways, local substance organization could become responsive to internal or outside stimulus or influence. Overnutrition, relative osmotic values of inclusions, dialysis as well as surface tension, — all these things are doubtless fruitful causes of origin and grouping of vesicular structures. Substance habit is clearly guided and to some extent controlled by chemical and physical conditionings, and it is likely that of all such opportunities the living substance organism neglects in the long run no one that fits in well with its inherent or established lines of habit. It is to be kept well in mind that as far as we can go in the series, the continuous substance is still complex organism with specific controls and habits and conditionings.

The greater stability of the coarser structure can create and support more stable activities, form, functions, tendencies, and

habits. In such a set of conditions the more patent organism has its origin. Now formation and function of substance organs being closely dependent on presence of specific materials, their origin and meaning cannot be wholly inferred from immediately existing conditions, but must be taken in relation to race habits of the substance. Functions directly possible to such organs are complex enough, but that strange interwoven chemical, physical and physiological causation spoken of in Heredity multiplies others intermingled with these. What causative influence may come into each substance organ from any side and from long distances of space and time, for instigation or support of any local habit, especially in the invisible series, cannot be known or guessed. The excretions of one substance organ can stimulate secretive function in another, near or remote, this may be in turn necessary for excretions of another such organ, and these again cause physiological activity, as of contraction or increased irritability, in still others, the products of which again act or react functionally elsewhere. The products of one minute set of vesicular functions may stimulate organs of a structure of Bütschli, and these again act upon grosser or compound organs, and each of all this series again react upon the primary substance organization. Iterated or long continued function of one set may be necessary for more rarely recurrent, or even chance, functions of another substance organ. Chemical products of invisible as well as visible substance organs may be held sealed in vesicles of the finer foam, and later find their way, by migrant interalveolar stuff or by blood vessels, to a perpetuation or other area, there to await interactions of many other substance organs before their turn for causative function arrives. The whole organism may be regarded as a compound and complex series of many vesicular organs for excretion and secretion as well as for irritability or contractility. In this, and in the rhythms of recurrence of function, all sorts and kinds of Atavism are rooted. Every vesicle whose walls are of living functioning substance is a true substance organ. It is secretory and excretory for this which is muscle and nerve. A final hypothetical vesicle whose walls should be a simple film and

pel certain relations of the mass or organism with the opportunities of external environment. It need no longer be regarded as meaning mental states, or as due to mental processes, for these, if present, are but part of the chain of interactions of substance organs. Apart from their incidental form as results of secondary substance function and vesicular organization, — instincts are peculiarly grouped as those interrelations of substance habit that result in *space-bridging and time-bridging relations of the mass or animal with its external opportunities.* They involve always intensification areas of ectosarcal organization, — indeed, but for these, I think instincts as such would be wholly unknown to us, remaining indistinguishable amongst other substance habits within the mass, where doubtless there are now hidden many kindred phenomena, having relation to the internal environment of the mass. For like all interrelations of the organism's parts, or of the mass with its external environment, instinct merely repeats in grosser terms radical powers and habits of the substance as such, expressed upon a secondary functional machinery.

Conclusion.

[151] To sum up; — the facts seem to warrant present belief that the living substance of all organisms is one physiologically continuous, living, plasma, homogeneous throughout in its intrinsic powers and properties, but having varied local and temporary habits of self-expression, which are largely, and inextricably correlated with physical and chemical conditionings of its form and composition as complex emulsive foam — yet not to be wholly identified with, nor wholly explained by, these. The organism as we have known it, is secondary, incidental, to the life-history of the protoplastic continuous substance of the living being: is result rather than cause of substance habit. Visible form and structure express only secondary truths. The part played in this state of things by purely physical and chemical conditions is doubtless enormous, but the wonder is not thereby lessened. If these results, or the physical terms in which they are presented, have

at moments seemed to make the living organism ever more and more an automatic result of physical and chemical adjustments and relations; — let me remind, nay, urge upon the reader, that behind and beyond this automatism, the living substance has been shown to be still unrevealed to us, still transcending existing arrangements though always by and through these expressing its unexplained, inherent, powers and properties. For in all structures, however relatively stable they seem to us, the protoplastic substance is always ready and eager for more radical physiological self-expression. And it is this substance that is the true organism, by whose secretions, excretions, and dispositions of its surplus material in an organized vesicular way, the secondary and more patent organism with which we are familiar is formed. Perhaps one of the most important things shown is that this protoplastic substance is everywhere capable of just such organization of its powers in relation to its internal opportunities, as produces in organisms, from the lowest to the highest, all perceptive intercourse with mass environment. We may limit the word perceptive to the lowest form of sentience, but in and from this can arise by gradations the highest sorts known to us, even apperception and idea. In other words the substance organism has within the limits of invisible vesicular organization all that is requisite for true physiological habits and instincts, akin to those of the patent organism. The simplest and most primitive form of living substance we can get, and the smallest sub-divisions of this we can see with the microscope, is still a complex organism functioning for the race-substance, — is still, old as the hills, and very wise.

In its inseparable physical form and chemical constitution lie the necessity and the temptation of a physical basis upon and through which to postulate the life phenomena of the living substance, since it expresses and must express itself through these conditionings. Because he has supplied in great part this intrinsic necessity of the science of biology, and in such form, that, with some extension and modification, it can be brought directly into relation with substance phenomena down to the smallest seen or inferred; — Bütschli deserves highest

gratitude and praise. Had it not been for his masterly work, these researches at least would not have been carried on so effectively, nor expressed in so unified a terminology which seems to add much to their value. I may say that, until after many repeated series of observations, I was quite neutral as to this vesicular theory, — if with any bias, was adverse to it.

The possible interaction of physical, chemical, and physiological conditions in so sensitive, so powerful, and so causative an arrangement as is found in the living emulsive foam, passes all imagination, and offers wonderful opportunities of evolution along lines of substance habit. For another interesting result of these researches would seem to be a re-birth of "natural selection," making this again appear the powerful agent in evolution of organisms that Darwin believed it to be. We must remember that he said, "*Natural Selection can act on every internal organ, on every shade of constitutional difference, on the whole machinery of life.*" His line of argument becomes perforce artificial wherever he attempts to decide the usefulness of any such difference solely in relation to the organism in which it is found. Again and again, being confronted with this difficulty of linking values of structural or functional differences with the life-history of the organism, Darwin was compelled to find escape along lines of benefit to the species of organisms, — and this truly brings the matter at once into the ground of my offered standpoint. Natural selection acting upon substance structures and substance organs dives deeper into life mysteries, is more searchingly constraining upon the race-history, than it ever could be by acting upon mere organism structures and organs, — that application of the theory must stumble and fail wherever it meets one of the many sacrifices of the unit for the substance organism as prime meaning or end. Instead of saying with Darwin "Natural selection it should never be forgotten can act in each part of each *being* solely through and for *its* advantage," I would say rather, 'through and for the advantage of the substance as such and especially as race organ.' Re-reading the Origin of Species, I have been amazed at elimination of what have always seemed like obscurities

of reasoning and radical difficulties. Understanding of sexual selection and of the correlation of parts and powers in organisms has also been much helped for me by the new set of facts, as to selection of environment by the substance as such, and as to interrelation of substance organs in creating the organism, as well as in expressing the substance's protoplastic functional life.

Reproduction is most helpful in race-history of the substance not alone by multiplying the race organs, but *by permitting the death of adult phases*, for thus it recurrently sets the substance free from trammels and limitations imposed upon it by that secondary machinery of the patent organism, its more intimate life and functions have created, which must limit its evolutionary progress as well as its continuance.

The offered standpoint is a most fruitful one; yet it is not an easy thing at once to assume it, and for a time the mental foothold must feel slippery. Man is so used to regard as property of the animal, all structure and function within its limits. Belonging to a standpoint of early and almost inevitable interpretation, and involving natural egotism of the unit, such mental custom is deep-rooted and difficult to overcome. A living being seems to be so patently master of its parts and powers, and these so clearly necessary to and for its existence; then too, — and here lies the root difficulty, — the coincidence of the external limits of the mass and of the animal, binds one to think of them as one and the same thing; the grosser structural subdivisions of the mass are plainly correlated with powers and functions of the animal we see. The simple, unconscious anthropomorphism of all our mental processes make this so natural a first standpoint, for how could the early self-conscious being escape a full and strong acceptance of himself as possessor and master of his parts and powers, — a belief that his directive influence in many ways, meant complete control. These things being true for himself, then the parts and powers of every other animal must as surely express a like self-ownership and a kindred coherence of meaning for it as unit.

Even the discovery of gross reflex actions, though a great shock to this primitive standpoint, has not displaced us from

it. And I think it will be long before most people will agree to think differently, before they will be willing to believe that all the structures and functions, visible and invisible, included in the skin of their familiar dog, or cat, or horse, do not peculiarly and wholly belong to that being, are not primarily for, and just to express, that individuality: — how otherwise explain the strange unity and purposive harmony of external features, of grosser or even minuter structural characters, or the interrelations of parts and powers, and of functions; then again these things mean normal life and function to the organism as such, deprivation of them means to it maimed or pathological states, or death even, and many of them are seen to act directly for and to subserve its existence. To ask man to think of these things as but incidental to minute, local, vesicular, organization and function of a protoplastic ground substance which must itself depend on that grosser organism for very continuance of life, — surely this is an unfair, even a ludicrous, demand upon human intelligence! To even the thinking public, the question raised must for a long time to come seem to be mere mental juggling — a sleight of idea trick, — or an effort to apply metaphysical methods and a mystical standpoint to biological fact. If the sum total of parts and powers included within an animal's limits are not indeed its own, are not for it, — whose and for what are they? Only three years back such a question would have seemed too absurd to be asked — may even yet seem so — and it is not many years since the means of perceiving or answering it have been in our hands. But I think to those, (they will be few), who will read with patient thought the long and minute record of selected facts in the foregoing pages, this question will not only thrust itself forward as it has done for me, but will bring with it an answer of sufficient assurance to swerve the trend of research more and more strongly toward the lines indicated.

The offered standpoint does not miss the utmost interdependence of parts and powers of any living unit, — it makes this more radically certain and clear than has yet been understood, showing that each and all are of value in the true organism's life; it does not hide from us that these form or maintain the

obvious creature, or that they are wholly dependent on it for continued existence, — but it discovers to us that this is but a small part of all, that the true organism is the invisible vesicular substance whose mass limits coincide of necessity with those of the living being; that all of the multiple parts and powers, functions and organs, of living units are, and primarily were, of and for the substance as such, and only partially and incidentally for the animal or plant: — in short that the zoölogical or botanical unit is in part a psychological formulation of mass separateness, while actually a vesicular accident or functional incident of the substance organism's protoplastic life.

The fruit of these researches, then, is discovery of a new biological standpoint with its terms. Though bringing no explanation of vital phenomena, they may, none the less, prove helpful, — after the manner of a perpetuation area, — by freeing the substance of our thought from trammels of that secondary, incidental, structure its very self-expression has wrought about it; and by re-embodying it in a younger and more plastic phase which, though it must bear out the race-history, may better meet our opportunities, and is less encumbered by excretions, and inorganic, inelastic, deposits of centuries of function.

Our old standpoint will not, and should not, be abandoned for the new — but this, once perceived, can never be forgotten or discarded. Research cannot spring wholly from one or from the other, but the interest of active workers will surge into the new or back to old paths as natural limitations of power and focussed effort block man's progress here or there. Flux and intermission and recurrence — these things pertain to all substance function from the lowest protoplastic to the highest perceptive — marking the very throb and pulse of livingness.

The mystery of life remains, — but at least it has had no light answer framed to meet it. "That which is is far off and exceeding deep; who can find it out?"

August, 1896.